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THE EFFECTS OF LEAFHOPPER FEEDING INJURY ON APPARENT PHOTOSYNTHESIS AND TRANSPIRATION OF APPLE LEAVES [1]

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INTRODUCTION

The leafhoppers that attack apples have received relatively little attention from investigators and growers, probably because they do not cause immediate injury to the fruit itself as do codling moths, curculios, and similar chewing insects, and probably, too, because their greatest injury to the leaves appears late in the season when the fruit is almost mature.

Two types of leafhopper injury occur on apple leaves: (1) A yellowish-green stippling on the upper leaf surface caused by species of *Typhlocyba, Erythroneura,* and some *Empoasca*—the mesophyll feeders (*1, 4, 9, 10, 11*)[3]; and (2) a yellowing, puckering, and wilting of the leaf caused by one or more species of *Empoasca*—the vein feeders (*11, 12, 13*).[4] There appear to be no published data which show the effects of vein- or mesophyll-feeding leafhoppers on the metabolic processes of apple leaves. The literature deals largely with descriptions of visible leaf injury (*3, 6, 8*).

It is the purpose in this paper to point out the effect of various degrees of leafhopper feeding injury on apparent photosynthesis and transpiration of apple leaves. Seasonal trends in leafhopper population and the effect of feeding injury on leaf anatomy also are discussed.

MATERIALS AND METHODS

The leafhoppers used in this study were collected from a large McIntosh apple tree growing in an experimental orchard in southern Indiana and were shipped to Ohio State University by special delivery in hardware-cloth cages. The time in transit was less than 24 hours. The cages were ellipse-shaped, about 10 inches in height by 4 inches in diameter, and were filled with damp excelsior and wrapped with cheesecloth. This technique was employed in all seasons of the year; fresh material was used in the cages in summer. The population counts were made at 8 evenly distributed locations on the tree (fig. 1) during the summer of 1940. One thousand leaves were inspected weekly for the tree as a whole, 5 groups of 25 leaves each at each of the 8 locations.

When the leafhoppers arrived at the laboratory, they were released into special cages which covered the shoots of potted Stayman Winesap

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[3] Italic numbers in parentheses refer to Literature Cited, p. 280.

[4] REED, T. W. THE APPLE LEAFHOPPERS OF WESTERN NEW YORK. 1933. [Unpublished thesis, Master of Science, Ohio State University, Columbus, Ohio.]

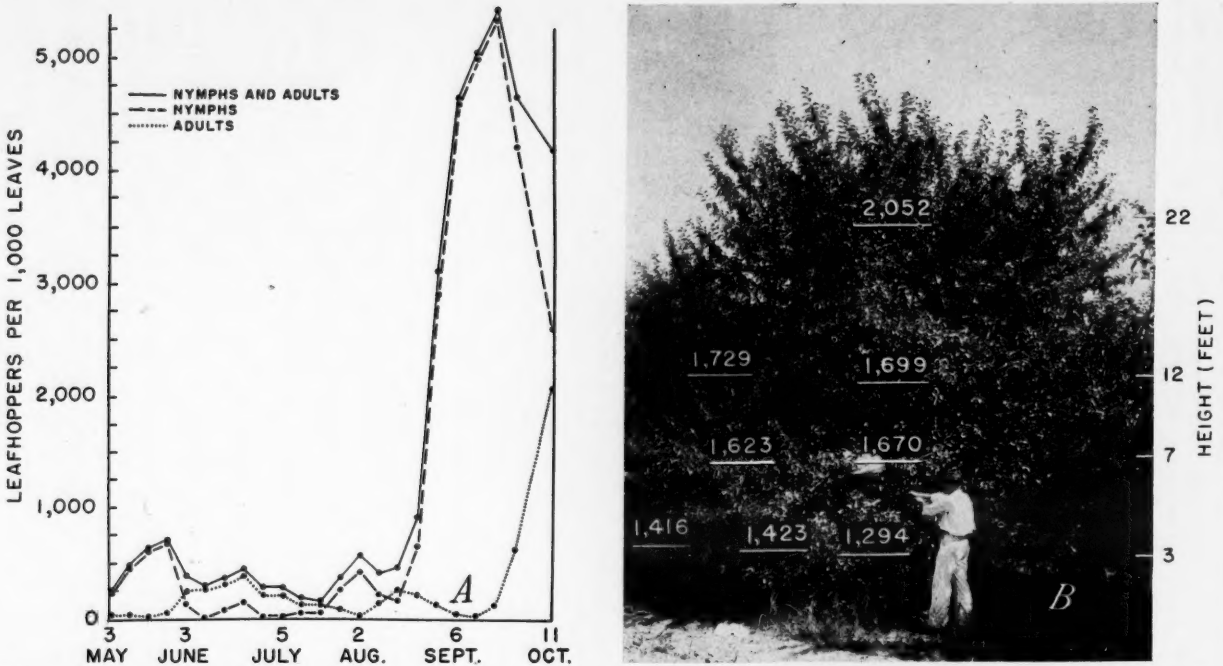

FIGURE 1.—*A*, Weekly population trend of leafhoppers on a McIntosh apple tree in southern Indiana during the 1940 season; *B*, the tree from which the leafhoppers were collected. The figures superimposed on the photograph are average numbers of insects per 1,000 leaves found each week in counts at 8 distributed locations at 3-, 7-, 12-, and 22-foot levels.

apple trees. The cages were made of ¼-inch-mesh hardware cloth covered with cheesecloth, and had small cellulose acetate windows through which the insects could be observed.

Photosynthesis and transpiration measurements were made at Ohio State University by the method of Heinicke and Hoffman (*7*), both outdoors and in the environment-control chamber (*2*). The metabolic activity of 12 leaves was studied in each experiment; 6 of the leaves were treated and 6 remained as checks. After a ratio between the rates of photosynthesis and transpiration of the 2 groups of leaves had been determined, a sleeve cage of insects was placed over one of the shoots as shown in figure 2. The insects were permitted to feed on the foliage for a given period, after which they were removed and the metabolism studies were resumed. Any change in the ratio after the feeding period as compared with the ratio before feeding was interpreted as the result of insect injury. The insects were permitted to feed at several successive periods in a given experiment.

Apple leaves upon which leafhoppers had been permitted to feed were examined microscopically, in cross section. The leaf material was mounted in paraffin, cut on a rotary microtome, and stained with Heidenhain's iron-alum haematoxylin.

Analysis of variance and significance of data were determined according to Fisher's tables for F and t.[5]

EXPERIMENTAL RESULTS

POPULATION STUDIES

Counts of leafhoppers in the experimental orchard were made each week, beginning May 3, 1940. After the overwintering population of *Erythroneura* species had died about the middle of May, *Typhlocyba pomaria* McA., the white apple leafhopper, was the only species present in significant numbers until late in the summer. The graph in figure 1 shows the weekly population of all leafhoppers, adults and nymphs, on the mature McIntosh tree. The first peak in the curve represents almost entirely the species *T. pomaria;* the second, several species of *Erythroneura;* the third, *T. pomaria* and some *Erythroneura;* and the last, *T. pomaria* and various species of *Erythroneura* in the ratio of 2.83 *T. pomaria* to 1 of Erythroneura. The figures on the photograph in figure 1, *B*, show the average number of leafhoppers per 1,000 leaves found each week in counts at the respective locations up to August 4, 1940. It will be noted that the insects were more abundant near the top of the tree.

Eggs of *Typhlocyba pomaria* were laid in the bark of 1- to 4-year wood in the fall and these overwintered before hatching; *Erythroneura* overwintered in the adult stage under leaves and other protective plant debris. Population counts of *Erythroneura* during the winter of 1939–40 revealed an average of 160 adults per square yard in fallen leaves and grass in the orchard. The leafhoppers were more numerous near the drip of the branches where ground cover was heavier.

EFFECTS ON PHOTOSYNTHESIS AND TRANSPIRATION OF APPLE LEAVES CAUSED BY FEEDING OF APPLE LEAFHOPPERS

One hundred leafhoppers per leaf were released in a sleeve cage over apple shoots after the pretreatment ratio for photosynthesis and transpiration had been established over a 3-day period. The insects were

[5] The statistical analyses were carried out under the direction of Mrs. Z. E. Alberts, Department of Zoology and Entomology, Ohio State University.

permitted to feed for 3 days, after which leaf activity was measured again. The data in table 1 and figure 3, *A*, show that the rate of photosynthesis was reduced 25 percent and transpiration 26.7 percent by the feeding of leafhoppers at the rate of 100 per leaf for 3 days, or 7,200 "leafhopper hours" per leaf (see fig. 4, *A*, *a*, for apparent leaf injury).

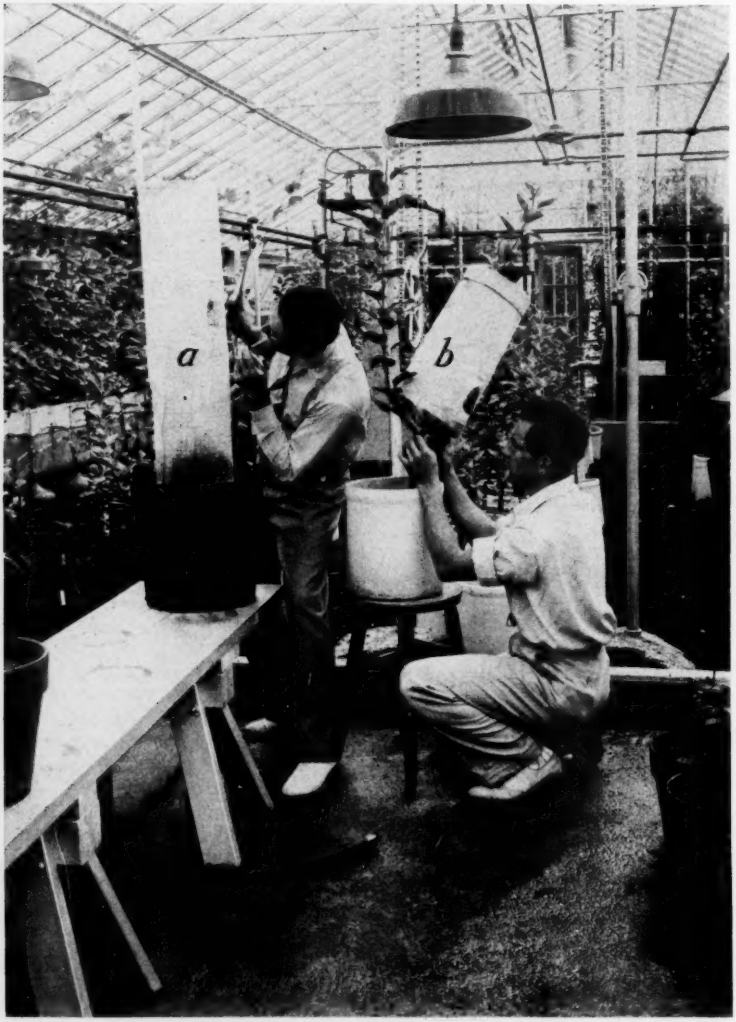

FIGURE 2.—Experimental trees with two shoots were grown in 5-gallon stone crocks; one of the shoots was used in the feeding experiment, the other served as a check. A definite number of insects per leaf were transferred from the stock cage (*a*) to the test cage (*b*) for each successive feeding period between photosynthesis-transpiration determinations.

TABLE 1.—*The effect of apple leafhopper injury on the rates of photosynthesis and transpiration of Stayman Winesap apple leaves, experiment A*

Date of leaf activity measurement [1]	CO_2 per cu. ft. of air	Photosynthesis (CO_2 per 100 cm.² per hour)		Test/Check ×100	Expected rate	H_2O per cu. ft. of air	Transpiration (H_2O per 100 cm.² per hour)		Test/Check ×100	Expected rate [2]
		Check	Test				Check	Test		
	Milligrams	*Milligrams*	*Milligrams*		*Percent* [2]	*Gram*	*Grams*	*Grams*		*Percent*
Mar. 3	19.9	10.5	14.0	102.9	.....	0.302	0.56	0.83	148.2	.....
Mar. 4	19.0	7.0	7.8	97.1	.....	.303	.94	1.18	125.5	.....
Mar. 5	18.0	17.5	20.8	118.3	.....	.292	1.10	1.50	136.4	.....
Average				106.1					136.7	
Mar. 9	19.2	15.1	15.9	105.3	99.3	.251	1.47	1.55	105.4	77.1
Mar. 10	17.4	13.9	9.1	65.5	61.8	.267	1.62	1.48	91.3	66.8
Mar. 11	17.7	12.9	11.7	90.7	85.5	.230	1.63	1.65	101.9	74.6
Mar. 12	17.1	13.1	7.5	57.3	54.0	.261	1.56	1.63	104.5	76.5
Average				79.7	75.1				100.7	73.8
Mar. 16						.255	1.58	1.77	112.0	82.0
Mar. 17	17.7	20.3	16.6	81.8	77.1	.257	1.60	1.62	101.3	74.1
Mar. 18						.249	1.62	1.68	103.7	75.9
Mar. 19	16.8	18.6	15.4	82.8	78.1	.231	1.97	1.43	72.6	53.1
Average				82.3	77.6				97.4	71.3
Apr. 1	17.3	12.3	10.0	81.3	76.6	.264	1.75	1.75	100.0	73.2
Apr. 2						.261	2.06	1.65	80.1	58.6
Apr. 3	18.2	14.1	11.9	84.4	79.6	.249	2.13	1.76	82.6	60.4
Apr. 4	16.5	15.0	13.9	92.7	87.4	.255	2.10	1.25	59.5	43.5
Apr. 5	18.2	15.8	11.3	71.1	67.0	.265	1.44	1.56	108.3	79.3
Apr. 6	18.3	15.8	12.7	80.4	75.8	.250	1.97	1.41	71.6	52.5
Average				82.0	77.3				83.7	61.2
Apr. 12	17.8	17.1	12.8	74.9	70.6	.262	1.80	1.77	98.3	71.9
Apr. 13	17.4	14.1	10.6	75.2	70.9	.257	1.83	1.82	99.5	72.8
Apr. 14	17.7	14.2	11.7	82.4	77.7	.253	1.83	1.54	84.2	61.6
Apr. 15	19.4	16.3	16.7	102.5	97.6	.261	1.47	1.20	81.6	59.7
Apr. 16	18.0	17.5	17.3	98.9	93.3	.254	1.13	.96	85.0	62.2
Apr. 19	17.7	14.0	9.9	70.9	66.9	.....	.....	.....	.....	.....
Average				84.3	74.3				89.7	65.6
Apr. 26	15.9	12.3	11.0	89.4	84.3	.250	1.64	1.55	94.5	69.1
Apr. 28						.256	1.83	1.33	72.1	52.7
Apr. 29	16.8	15.5	6.3	40.6	38.3	.248	1.86	1.64	88.2	64.5
Apr. 30	16.5	15.1	8.8	58.3	55.0	.251	1.92	1.53	79.7	58.3
May 1	17.3	12.0	7.3	60.8	57.3	.250	1.90	1.35	71.1	52.0
May 2	17.7	14.5	6.6	45.5	42.9	.228	2.32	1.78	76.7	56.1
Average				58.9	55.8				80.4	59.6
May 21	16.5	4.4	.9	20.5	19.3	.216	1.32	.93	70.5	51.5
May 22	15.6	6.3	0	0	0	.269	1.18	.76	64.4	47.0
May 23	16.3	8.3	3.6	43.4	40.9	.275	1.14	.75	65.8	48.2
Average				21.3	20.1				66.9	48.9

ANALYSIS OF VARIANCE OF $\frac{\text{TEST}}{\text{CHECK}} \times 100$

Item	Degrees of freedom	Sum of squares	Mean of squares	*F*	Remarks
Photosynthesis	6	14,158.62	2,359.8	3.27	Significant.
	21	15,174.66	722.6		
Transpiration	6	9,553.04	1,592.2	10.54	Highly significant.
	24	3,626.39	151.1		

[1] Between each series of measurements the leafhoppers were permitted to feed.

[2] $\frac{\text{Test after treatment}}{\text{Check after treatment}} \times \frac{\text{Check before treatment}}{\text{Test before treatment}} \times 100 = \text{Percent expected rate}$

From these data it could be inferred that 300 leafhoppers per leaf (assuming a constant area of about 50 cm.^{2} for all leaves) may cause a reduction in photosynthesis and transpiration of about 1 percent in 1 hour.

Further injury (fig. 4, *A*, *b*) on the same leaves did not cause a significant reduction in either process. It was not until 4 weeks of

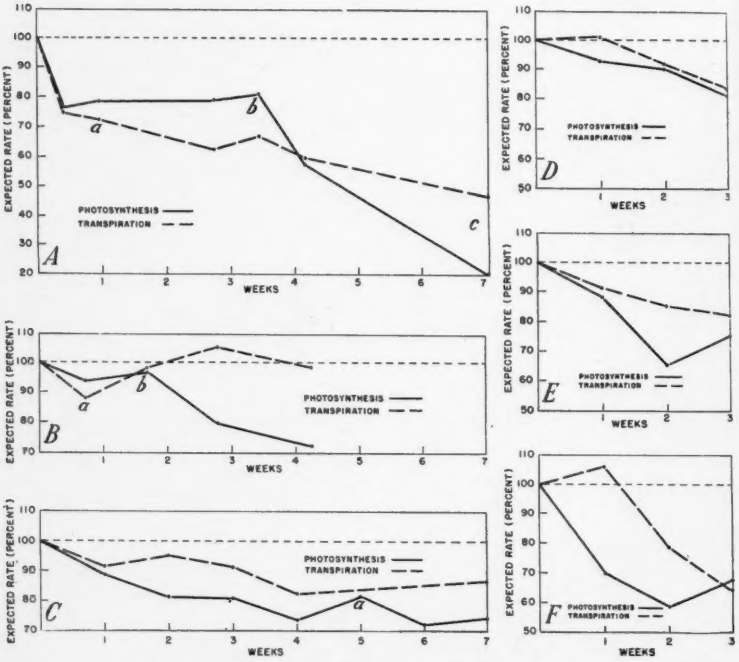

FIGURE 3.—*A*, *B*, *C*, *D*, and *E*, based on data from experiments of similar designation, show the effects of mesophyll-feeding by apple leafhoppers on apparent photosynthesis and transpiration of Stayman Winesap apple leaves. *F* shows the effect of the vein-feeding potato leafhopper, *Empoasca fabae*, on apple leaf metabolism. The value 100 represents photosynthesis and transpiration of the check leaves for every determination.

feeding with a slightly reduced insect population that further measurable reductions occurred. Seven weeks of feeding reduced the rate of photosynthesis 80 percent and transpiration 56.2 percent. At this time the leaves appeared severely injured; the surfaces were yellowish green, the spots had coalesced over the entire area, and there was a slight curling and burning at the margins (fig. 4, *A*, *c*). The

reduction in photosynthesis was significant and in transpiration highly significant.

EXPERIMENT B

In similar experiments but with a smaller population of insects (50 to 60 per leaf), there was a reduction in photosynthesis but the

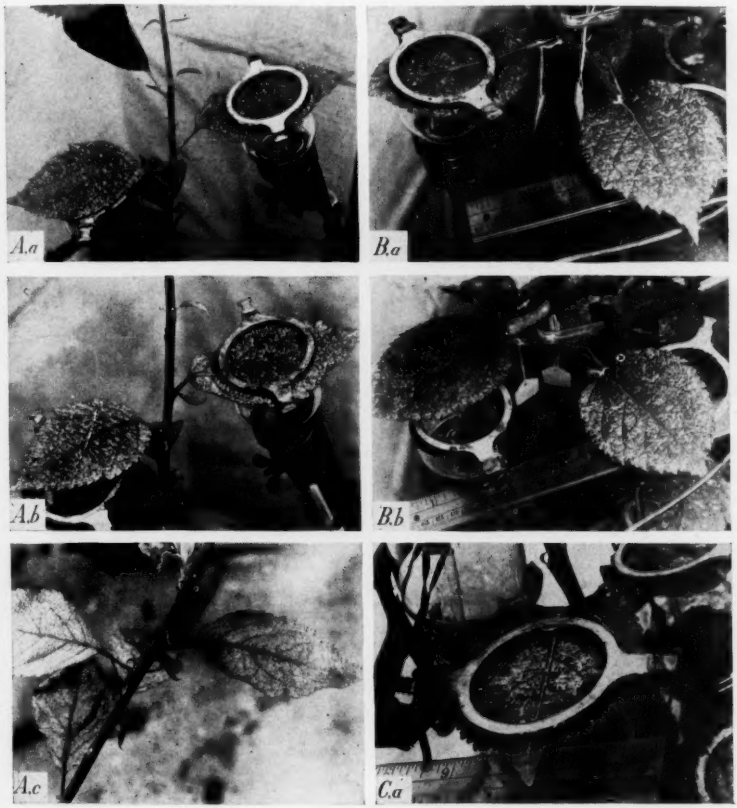

FIGURE 4.—Stages of feeding injury at positions marked on the photosynthesis-transpiration curves in figure 3; for example, *A*, *a*, shows apparent feeding injury when photosynthesis was reduced approximately 25 percent and transpiration 27 percent as indicated at point *a* in figure 3, *A*.

rate of transpiration was not significantly affected (table 2, fig. 3, *B*). Four weeks of feeding was accompanied by a significant reduction in photosynthesis of 26.4 percent. (See fig. 4, *B*, *a*, and *B*, *b*, for apparent injury at stages specified in fig. 3, *B*.)

TABLE 2.—*The effects of apple leafhopper injury on the rates of photosynthesis and transpiration of Stayman Winesap apple leaves, experiment B*

Date of leaf activity measurement [1]	CO_2 per cu. ft. of air	Photosynthesis (CO_2 per 100 cm.² per hour)		Test/Check ×100	Expected rate	H_2O per cu. ft. of air	Transpiration (H_2O per 100 cm.² per hour)		Test/Check ×100	Expected rate [2]
		Check	Test				Check	Test		
	Milligrams	*Milligrams*	*Milligrams*		*Percent* [2]	*Gram*	*Grams*	*Grams*		*Percent*
Mar. 16	19.4	19.4	19.3	99.5						
Mar. 17	16.4	22.1	22.2	100.5		0.248	1.78	1.46	82.0	
Mar. 18	16.4	16.5	15.5	93.9		.240	1.81	1.69	93.4	
Mar. 19	17.6	18.3	17.9	97.8		.237	1.87	1.66	88.8	
Average				97.9					88.1	
Mar. 26	18.0	19.7	20.1	102.0	104.0	.244	1.33	1.06	80.0	90.8
Mar. 27	20.7	29.0	28.1	97.0	99.1	.252	1.31	.92	70.2	80.0
Mar. 28	22.4	24.6	18.0	73.2	74.7	.269	1.47	1.48	100.7	114.3
Mar. 29	17.7	16.9	17.6	104.1	106.3	.260	1.69	1.25	74.0	84.0
Mar. 30	17.2	17.0	13.7	80.6	82.3	.279	1.59	1.38	86.8	98.5
Mar. 31	16.9	12.2	12.7	104.1	106.3	.251	1.12	.84	75.3	85.5
Average				93.5	95.5				81.2	92.2
Apr. 7	18.6	15.1	14.4	95.3	97.4	.258	1.44	1.33	92.4	105.0
Apr. 8	17.0	14.6	15.7	107.5	109.8	.241	1.85	1.74	94.1	106.8
Apr. 9	16.8	15.3	13.4	87.8	89.7	.260	1.58	1.55	98.1	111.4
Apr. 10	18.2	10.4	10.1	97.1	99.2	.246	1.22	1.02	83.6	94.9
Apr. 11						.259	1.46	1.27	87.0	98.8
Average				96.9	99.8				91.0	103.4
Apr. 20	30.6	23.5	16.7	71.1	72.6	.250	.86	.88	102.3	116.1
Apr. 21	25.6	22.2	18.5	83.3	85.1	.256	1.21	1.26	104.1	118.2
Apr. 22	17.5	14.7	11.9	81.0	82.7	.252	1.39	1.29	92.8	105.3
Apr. 23	17.9	13.4	9.5	70.9	72.4	.253	1.61	1.52	94.4	107.2
Apr. 24	15.9	14.7	11.6	78.9	80.6	.248	1.47	1.55	105.4	119.6
Apr. 25	18.1	24.0	21.1	87.9	89.8	.262	1.63	1.48	90.8	103.1
Average				78.9	80.5				98.3	111.6
May 5	16.3	14.3	10.0	69.9	71.4	.259	1.66	1.61	92.0	110.1
May 6	15.8	11.2	10.6	94.6	96.6	.259	1.98	1.59	80.3	91.1
May 7	17.7	14.1	7.3	51.8	52.9	.277	1.81	1.74	96.1	109.1
Average				72.1	73.6				92.5	103.4

ANALYSIS OF VARIANCE OF $\frac{\text{TEST}}{\text{CHECK}} \times 100$

Item	Degrees of freedom	Sum of squares	Mean of squares	F	Remarks
Photosynthesis	4	2153.45	538.36	4.28	Significant.
	18	2263.59	125.76		
Transpiration	4	901.98	225.5	3.40	Significant variance but not a reduction.
	18	1197.42	66.37		

[1] Between each series of measurements the leafhoppers were permitted to feed.
[2] See footnote 2, table 1, for method of calculation.

Experiments C and D

Experiments were run on experimental leaves in the laboratory to duplicate the population of insects in the field. At the time weekly population counts were made in the field, leafhoppers (adults and nymphs) were collected and shipped from the Indiana orchard to the environment-control chamber. The concentration of insects, species ratio, and interval between changes in insect population on the test leaves were adjusted to make the duration of the experiment in the laboratory shorter than an entire summer season. The data can be interpreted, however, as typical of the results of a season of leafhopper activity.

The technique employed in handling the leafhoppers in these experiments differed from that in the previous experiments. The leafhoppers were released in the leaf cups (7) on the lower surfaces of the apple leaves instead of in cheesecloth cages. According to Wigglesworth (*14, p. 198*), insects respire at the rate of approximately 3 mg. of carbon dioxide per gram of insect weight per hour. A leafhopper, then, would respire about 0.015 mg. of carbon dioxide per hour. At this rate the maximum number of leafhoppers per leaf at any time in the course of the 2½-hour determination would not respire enough carbon dioxide to interfere with the photosynthesis measurements. Thus, the insects were permitted to feed continuously even during the determinations and were confined to the part of the leaf surface included by the leaf cup rather than to all the surface included in a sleeve cage.

The data in table 3 and figure 3, *C*, show that at a point in the experiment corresponding to May 17 in the field, photosynthesis was reduced 16.5 percent and transpiration 4.9 percent. At a point corresponding to June 25 the reductions were, respectively, 19.2 and 13.8 percent, and by July 26 they were 27.1 and 12.9 percent. It would appear from these data that before mid-July, when the insect population is still rather low, marked reductions may occur in the rate of photosynthesis, especially in the early part of the period. The gradual reduction in photosynthesis recorded from week to week in experiment C was not significant, but the final reduction at a point corresponding to July 26 was highly significant (see fig. 4, *C, a*, for apparent injury toward end of experiment). The reduction in transpiration was not significant. In experiment D (table 4 and fig. 3, *D*), which was carried only to a point corresponding to June 5 in the field, reductions in transpiration and photosynthesis, although not significant, were recorded.

Experiment E

Table 5 and figure 3, *E*, show the results of a fifth experiment with the various species of apple leafhoppers. This experiment yielded data similar to those in the experiments described above. Three feeding periods with a population of approximately 25 leafhoppers per leaf brought about a reduction in the rate of photosynthesis of 23.8 percent and in transpiration of 16.5 percent. The reduction in transpiration over the entire period of the experiment was significant; the reduction in photosynthesis was significant from one feeding period to the next and highly significant over the 3-week period.

TABLE 3.—*The effects of apple leafhopper injury on the rates of photosynthesis and transpiration of Stayman Winesap apple leaves, experiment C*

Date of leaf activity measurement [1]	CO_2 per cu. ft. of air	Photosynthesis (CO_2 per 100 cm.² per hour)		Test / Check ×100	Expected rate	H_2O per cu. ft. of air	Transpiration (H_2O per 100 cm.² per hour)		Test / Check ×100	Expected rate [2]
		Check	Test				Check	Test		
	Milligrams	*Milligrams*	*Milligrams*		*Percent* [2]	*Grams*	*Grams*	*Grams*		*Percent*
May 25	17.0	14.3	24.6	172.0	.....	0.212	1.49	1.97	132.2	.....
May 26	16.3	14.5	20.1	138.6	.....	.200	1.56	2.06	132.1	.....
May 27	17.4	14.8	24.6	166.2	.....	.224	1.35	1.86	137.8	.....
May 28	16.8	15.3	23.9	156.2	.....	.215	1.51	2.07	137.1	.....
May 29	14.8	11.0	18.0	163.6	.....	.217	1.39	1.78	134.3	.....
Average	.....	.....	.....	159.3	.....	.....	.....	.....	133.5	.....
May 30	15.2	19.0	28.5	150.0	94.2	.212	1.69	1.99	117.8	88.2
May 31	15.5	20.3	26.0	128.1	80.4	.191	1.40	1.82	130.0	97.8
June 1	14.8	17.3	23.0	133.0	83.5	.185	1.56	1.90	121.8	91.2
June 2	14.9	18.8	25.7	136.7	85.8	.175	1.64	2.31	140.9	105.5
June 3	16.4	18.4	24.6	133.7	84.0	.182	1.69	1.96	116.0	86.9
June 4	17.3	16.3	25.6	157.1	98.7	.189	1.63	1.85	113.5	85.0
June 5	15.5	13.4	21.2	158.2	99.3	.233	1.44	1.66	115.3	86.4
June 7	17.6	18.7	25.8	138.0	86.7	.215	1.35	1.50	111.1	83.2
June 8	16.2	14.4	20.6	143.1	89.9	.573	1.12	1.79	159.8	119.7
June 9	17.7	21.0	29.1	138.6	87.0	.192	1.53	2.18	142.5	106.7
June 10	17.8	17.1	26.1	152.6	95.8	.181	1.55	2.03	131.0	98.3
June 11	17.9	34.9	43.4	124.4	78.1	.185	1.64	2.18	132.9	99.5
June 15	16.6	11.5	15.6	135.7	85.2	.....	.....	.....	.....	.....
June 16	16.6	15.2	15.7	103.3	64.9	.....	.....	.....	.....	.....
June 17	17.7	16.6	22.9	138.0	86.7	.....	.....	.....	.....	.....
June 18	17.1	13.2	22.1	167.4	105.1	.....	.....	.....	.....	.....
June 19	16.5	10.2	13.4	131.4	82.5	.385	1.38	1.70	123.2	92.3
June 20	16.5	11.2	14.9	133.0	83.5	.279	3.83	4.10	107.0	80.1
June 21	18.4	19.9	23.4	117.6	73.9	.405	1.23	1.53	119.5	89.5
June 22	15.7	13.7	14.3	104.4	65.6	.406	1.54	2.02	131.2	98.3
June 23	15.2	10.7	12.3	115.0	72.2	.430	1.31	1.68	128.2	96.0
June 24	15.1	5.9	8.5	144.1	90.5	.418	1.09	1.35	123.9	92.8
June 25	15.0	9.5	11.5	121.1	76.1	.409	1.21	1.42	117.4	87.9
June 27	15.9	16.0	15.6	97.5	66.8	.414	1.23	1.44	117.1	87.1
June 28	15.1	8.3	11.6	139.8	95.8	.414	1.28	1.26	98.4	79.4
June 29	15.3	12.4	13.3	107.3	73.5	.415	1.27	1.27	109.4	88.3
June 30	15.9	7.0	8.8	125.7	86.1	.415	1.16	1.32	113.8	91.8
July 1	17.1	10.3	9.7	96.1	65.8	.504	1.18	1.19	100.8	81.4
July 2	14.4	11.0	11.0	100.0	68.5	.316	1.03	.95	92.2	82.7
July 3	17.0	13.7	18.8	137.2	87.7	.403	2.08	2.35	113.0	88.4
July 8	16.1	7.2	11.6	161.1	102.9	.459	1.25	1.66	132.8	104.1
July 9	16.7	10.6	12.9	121.7	77.8	.464	1.25	1.50	122.0	95.6
July 10	18.3	12.5	16.0	128.0	81.8	.....	.....	.....	.....	.....
July 11	16.5	16.0	14.1	141.0	90.1	.....	.....	.....	.....	.....
July 13	16.8	11.7	11.6	99.1	63.3	.....	.....	.....	.....	.....
July 14	17.4	13.4	17.3	129.1	82.5	.....	.....	.....	.....	.....
July 15	21.1	15.2	22.7	149.3	95.4	.....	.....	.....	.....	.....
July 16	15.0	7.4	8.8	118.9	76.0	.....	.....	.....	.....	.....
July 17	15.8	9.5	8.6	90.5	57.8	.....	.....	.....	.....	.....
July 18	18.2	11.2	11.5	102.7	65.6	.....	.....	.....	.....	.....
July 19	21.7	14.2	12.4	87.3	55.8	.....	.....	.....	.....	.....
July 20	18.4	10.5	15.6	148.6	95.0	.404	1.21	1.37	113.2	88.7
July 23	16.4	10.7	12.1	113.0	80.8	.....	.....	.....	.....	.....
Average	.....	.....	.....	127.9	81.8	.....	.....	.....	120.5	92.2

ANALYSIS OF VARIANCE OF $\frac{\text{TEST}}{\text{CHECK}} \times 100$

Item	Degrees of freedom	Sum of squares	Mean of squares	*F*	Remarks
Photosynthesis	1	4,407.5	4,407.5	10.93	Highly significant.
	46	18,548.8	403.2		
Transpiration	1	870.1	870.1	1.65	Not significant.
	31	44,461.7	1,434.3		

[1] Leafhoppers were permitted to feed (field concentration) continuously even during the determinations.
[2] See footnote 2, table 1, for method of calculation.

TABLE 4.—*The effects of apple leafhopper injury on the rates of photosynthesis and transpiration of Stayman Winesap apple leaves, experiment D*

Date of leaf activity measurement [1]	CO_2 per cu. ft. of air	Photosynthesis (CO_2 per 100 cm.² per hour)		Test/Check ×100	Expected rate	H_2O per cu. ft. of air	Transpiration (H_2O per 100 cm.² per hour)		Test/Check ×100	Expected rate [2]
		Check	Test				Check	Test		
	Milligrams	*Milligrams*	*Milligrams*		*Percent* [2]	*Gram*	*Gram*	*Gram*		*Percent*
June 15	16.1	17.3	22.3	128.9	.....	0.177	1.77	2.20	124.3	.....
June 16	15.6	15.0	19.2	128.0	.....	.207	1.67	1.79	107.2	.....
June 17	17.7	19.3	23.2	120.2	.....	.234	1.72	1.82	105.8	.....
June 18	16.1	17.7	22.7	128.2	.....	.201	1.63	1.76	108.0	.....
June 20	16.5	16.7	21.5	128.7	.....	.389	2.40	2.50	104.2	.....
June 21	.....	.....	.....	.....	.....	.357	2.61	2.80	107.3	.....
June 23	.....	.....	.....	.....	.....	.371	2.34	2.61	111.5	.....
June 24	14.5	13.8	17.3	125.4	.....	.450	1.72	1.80	104.7	.....
June 25	14.7	11.3	13.7	120.2	.....	.374	2.04	2.30	112.7	.....
Average	.....	.....	.....	125.7	.....	.....	.....	.....	109.3	.....
June 28	13.9	17.8	17.2	96.6	76.8	.377	2.16	2.48	114.8	105.6
June 29	.....	.....	.....	.....	.....	.401	2.07	2.35	113.5	104.4
June 30	14.9	20.7	24.9	120.3	95.7	.385	1.88	2.15	114.4	105.1
July 1	.....	.....	.....	.....	.....	.324	1.59	1.82	114.5	105.2
July 2	15.2	12.1	15.6	128.9	102.6	.379	1.96	1.93	98.5	90.7
July 3	14.3	15.9	17.1	107.6	85.6	.371	1.81	2.21	122.1	112.2
July 8	15.8	9.7	13.4	138.1	109.9	.404	1.92	2.35	122.5	112.5
July 9	14.9	10.3	9.6	93.2	74.1	.408	1.92	1.82	94.8	87.1
July 11	14.8	10.6	13.6	128.3	102.1	.....	.....	.....	.....	.....
July 12	.....	.....	.....	.....	.....	.367	1.87	1.96	104.8	96.3
July 13	16.2	10.1	12.2	120.8	96.2	.335	2.48	2.54	102.4	94.1
July 14	16.1	12.8	15.5	121.1	96.4	.313	2.09	2.18	104.3	95.9
July 15	14.4	9.6	10.1	105.2	87.7	.342	1.82	1.99	109.3	100.4
July 16	14.6	10.9	13.6	124.2	103.8	.334	2.14	2.12	99.1	84.5
July 17	14.9	11.9	9.9	83.2	65.1	.....	.....	.....	.....	.....
July 18	15.0	12.8	16.0	125.0	97.8	.236	2.01	2.03	101.0	97.0
July 20	14.0	12.6	13.3	105.6	82.7	.350	1.90	1.79	94.2	90.4
July 21	14.0	8.0	8.9	111.3	87.1	.348	1.67	1.70	101.8	97.7
July 22	14.2	13.3	10.0	75.2	58.9	.332	1.86	1.70	91.4	87.7
July 23	15.4	10.4	13.1	126.0	98.7	.312	1.96	1.49	76.0	73.0
Average	.....	.....	.....	112.8	89.5	.....	.....	.....	99.1	96.7

ANALYSIS OF VARIANCE OF $\frac{\text{TEST}}{\text{CHECK}} \times 100$

Item	Degrees of freedom	Sum of squares	Mean of squares	*F*	Remarks
Photosynthesis	1	868.3	868.3	3.85	Reduction, but not significant.
	22	4,960.1	225.5		
Transpiration	1	208.2	208.2	2.36	Reduction, but not significant.
	26	2,292.6	88.2		

[1] Leafhoppers were permitted to feed (field concentration) continuously even during the determinations.
[2] See footnote 2, table 1, for method of calculation.

TABLE 5.—*The effects of apple leafhopper injury on the rates of photosynthesis and transpiration of Stayman Winesap apple leaves, experiment E*

Date of leaf activity measurement [1]	CO_2 per cu. ft. of air	Photosynthesis (CO_2 per 100 cm.² per hour)		$\frac{Test}{Check} \times 100$	Expected rate	H_2O per cu. ft. of air	Transpiration (H_2O per 100 cm.² per hour)		$\frac{Test}{Check} \times 100$	Expected rate [2]
		Check	Test				Check	Test		
	Milligrams	*Milligrams*	*Milligrams*		*Per cent* [2]	*Grams*	*Grams*	*Grams*		*Per cent*
Aug. 2	16.9	30.1	32.3	107.3	.....	0.416	3.11	2.90	93.2	.....
Aug. 3	15.5	18.6	19.8	106.5	.....	.384	2.43	2.42	99.6	.....
Aug. 4	15.9	24.9	26.2	105.2	.....	.405	2.15	1.88	87.8	.....
Average	.....	.....	.....	106.3	.....	.....	.....	.....	93.4	.....
Aug. 14	16.4	25.2	23.4	92.9	87.4	.416	2.82	2.24	79.4	85.0
Aug. 15	15.9	25.1	24.8	98.8	93.0	.452	2.97	2.58	86.9	93.0
Aug. 18	16.1	18.4	17.4	94.6	89.0	.386	3.28	3.15	96.0	102.7
Average	.....	.....	.....	95.4	89.8	.....	.....	.....	87.4	93.6
Sept. 1	18.1	15.5	10.6	68.4	64.4	.340	2.84	2.61	91.9	98.3
Sept. 2	16.8	19.6	11.5	58.7	55.2	.332	2.46	1.88	76.4	81.7
Sept. 3	21.1	18.5	15.5	83.8	78.9	.410	2.45	1.87	76.3	81.6
Average	.....	.....	.....	70.3	66.2	.....	.....	.....	81.5	87.2
Sept. 9	.....	.....	.....	.....	.....	.436	1.81	1.30	71.8	76.8
Sept. 10	16.5	12.3	12.2	99.2	93.3	.427	2.54	2.06	81.1	86.8
Sept. 11	15.9	15.6	9.8	62.8	49.5	.434	2.23	1.69	75.8	81.1
Average	.....	.....	.....	81.0	71.3	.....	.....	.....	77.9	81.6

ANALYSIS OF VARIANCE OF $\frac{TEST}{CHECK} \times 100$

Item	Degrees of freedom	Sum of squares	Mean of squares	*F*	Remarks
Photosynthesis	1	1,249.8	1,249.8	11.76	Highly significant.
	9	956.4	106.3		
Transpiration	1	277.8	277.8	5.26	Significant.
	10	528.6	52.9		

[1] Between each series of measurements the leafhoppers were permitted to feed.
[2] See footnote 2, table 1, for method of calculation.

EFFECTS ON PHOTOSYNTHESIS AND TRANSPIRATION OF APPLE LEAVES CAUSED BY FEEDING OF THE POTATO LEAFHOPPER

EXPERIMENT F

The potato leafhopper (*Empoasca fabae* (Harr.)) is among the least common of the species that occur in the orchard, but the injury that is causes is easily identified. The typical feeding puncture is made in the vascular system of the leaf or stem and this usually results in blocking the conducting tissues (*11*). The leaf area distal to the point of injury becomes pale green in a triangular area bounded by veins and the leaf margin. Only mature leaves were used in this experiment to avoid the typical curling that results from the feeding of *E. fabae* on leaves that have not reached full size.

In a typical experiment about 10 to 15 leafhoppers per leaf were released in the cheesecloth cage over the apple shoot, after a relation-

ship in metabolism had been established between the two groups of leaves. The insects were permitted to feed for a week. Apparent photosysthesis was reduced 29.1 percent, but there was no significant effect on transpiration (table 6 and fig. 3, *F*). Two additional feeding periods were accompanied by a reduction in the rate of photosynthesis of 31.1 percent and in transpiration of 33.6 percent. At this time the leaves exhibited the characteristic pale-green areas as the only external symptom of injury. The data for transpiration and photosynthesis were found to be significant and highly significant, respectively.

TABLE 6.—*The effects of potato leafhopper ((Empoasca fabae H.) injury on the rates of photosynthesis and transpiration of Stayman Winesap apple leaves, experiment F*

Date of leaf activity measurement [1]	CO_2 per cu. ft. of air	Photosynthesis (CO_2 per 100 cm.² per hour)		$\frac{\text{Test}}{\text{Check}} \times 100$	Expected rate	H_2O per cu. ft. of air	Transpiration (H_2O per 100 cm.² per hour)		$\frac{\text{Test}}{\text{Check}} \times 100$	Expected rate [2]
		Check	Test				Check	Test		
	Milligrams	*Milligrams*	*Milligrams*		*Percent* [2]	*Grams*	*Grams*	*Grams*		*Percent*
July 29	13.5	16.1	20.1	124.8		0.533	3.85	3.83	99.5	
July 30	15.5	19.0	23.3	122.6						
Aug. 1	15.6	16.4	16.6	101.2		.405	2.18	2.48	113.8	
Aug. 2	15.7	12.0	14.6	121.7		.393	1.22	1.71	140.2	
Aug. 5	13.8	19.4	20.2	104.1		.248	5.31	6.64	125.0	
Average				114.9					119.6	
Aug. 14	15.9	13.0	9.6	73.8	64.2	.501	2.47	2.80	113.1	94.8
Aug. 15	14.8	13.9	11.1	79.9	69.5	.463	1.90	2.83	148.9	124.5
Aug. 18	15.8	15.0	13.6	90.7	78.9	.575	2.48	3.02	121.8	101.8
Average				81.5	70.9				128.0	107.0
Aug. 31	14.6	15.3	8.4	54.9	47.8	.335	3.60	3.22	89.4	74.7
Sept. 1	13.2	15.9	10.9	68.6	59.7					
Sept. 2						.361	2.54	2.79	109.4	91.5
Sept. 3	16.2	15.9	12.5	78.6	68.3	.370	3.54	3.04	85.9	71.3
Average				79.2	58.6				78.4	87.4

ANALYSIS OF VARIANCE OF $\frac{\text{TEST}}{\text{CHECK}} \times 100$

Item	Degree of freedom	Sum of squares	Mean of squares	*F*	Remarks
Photosynthesis	1	4,856.1	4,856.1	43.8	Highly significant.
	12	1,331.0	110.9		
Transpiration	1	1,020.0	1,020.0	1.68	Not significant.
	11	6,684.2	607.7		

[1] Between each series of measurements leafhoppers were permitted to feed.
[2] See footnote 2, table 1, for method of calculation.

EFFECTS ON INTERNAL STRUCTURE OF APPLE LEAVES CAUSED BY THE FEEDING OF APPLE LEAFHOPPERS

Microscopic examination of moderately injured leaves revealed small groups of empty palisade cells, often with one or two uninjured cells in the center of each group. The cell walls appeared intact, although minute punctures through which cell contents were removed probably were present. Figure 5 shows cross sections of two apple leaves from which the cell contents of the upper palisade layer have been removed. Figure 5, *B*, shows an apple leafhopper killed, embedded, and sectioned in situ. The proboscis was lost in sectioning, but empty cells in the palisade layer show where the insect was feeding. During the progress

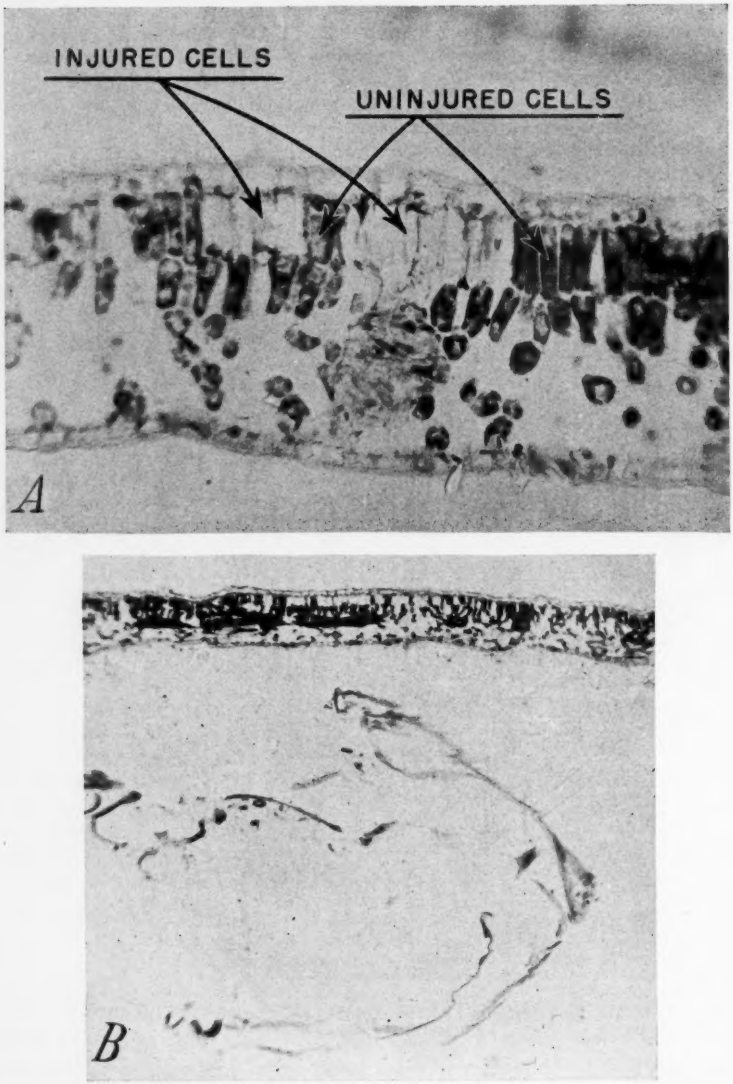

FIGURE 5.—Cross sections of Stayman Winesap apple leaves showing white apple leafhopper (*Typhlocyba pomaria*) feeding injury: *A*, Injured and uninjured cells of the palisade layer; *B*, cross section of leafhopper head in feeding position on under side of leaf, showing relative size of the insect and the cells upon which it has fed.

of these investigations a paper was published (*11*) in which somewhat similar results with apple leaves were reported. Smith and Poos (*12*) have pointed out that a small group of uninjured cells is often found in the center of a group of several injured ones where a leafhopper has been feeding.

Leafhopper injury caused a reduction in the thickness and fresh weight of apple leaves. Several hundred leaves were weighed and examined under the microscope in the field. Severely injured Black Twig leaves weighed approximately one-half as much (0.063 gm.) per unit area as uninjured leaves (0.123 gm.); they were from 0.097 to 0.120 mm. thick as compared with a thickness of 0.149 to 0.193 mm. in uninjured leaves.

DISCUSSION

In most instances considerable stippling was evident on the upper surfaces of the leafhopper-injured leaves before appreciable reductions in apparent photosynthesis and transpiration were recorded. A study of cross sections of injured leaves (fig. 5) shows that the spongy mesophyll tissue, in which probably a large part of the photosynthetic activity is carried on, is not affected until the palisade layers are markedly injured. When injured leaves are viewed from beneath by transmitted light, it is apparent that more light passes through the small injured spots than through the uninjured areas. It can be assumed, then, that that part of a leaf (spongy mesophyll cells) immediately under an injured area (palisade cells) receives more light after injury than it did before and conditions may be more favorable for photosynthesis in this region.

A given number of potato leafhoppers had a more detrimental effect on the metabolic activity than an equal number of leafhoppers of other species; this is in agreement with the data of Smith and Poos (*12*). In almost every case the leafhopper injury, whether of the vein or mesophyll type, affected the rate of photosynthesis more than the rate of transpiration, and usually sooner. An examination of the injured leaves showed that the moderately injured areas were low in active chlorophyll, although in other respects they appeared normal, at least morphologically. Thus, while photosynthesis might be reduced in these areas because of relatively low chlorophyll content, the loss of water vapor could go on at a rate more nearly normal. Severe injury by the potato leafhopper (*Empoasca fabae*) or by apple or grape leafhoppers (*Typhlocyba* spp. and *Erythroneura* spp.) ultimately resulted in a reduction in transpiration, associated with a blocking of the vascular tissues in the case of *Empoasca* (*11*, *12*, *13*,) [6] and a breakdown of the mesophyll cells in the case of the other two (*5*, *11*, and others).[6]

The decrease in leaf weight and thickness associated with leafhopper injury evidently results from the removal of the cell contents and the eventual drying and partial collapse of the injured cells. The total number of cells is probably not affected by leafhopper injury on a given leaf, as the leaf is a primary body; however, it is assumed that reduced vigor of the infested plant brought about by continued high populations of leafhoppers will eventually result in smaller leaves and other plant parts, especially the fruits.

[6] See footnote 4.

The question may arise as to which is more important to the welfare of the leaf—reduction in photosynthesis and transpiration caused by spray materials used to control the leafhopper, or injury from the insect itself. In practically all of the writers' experiments with nicotine sprays (data unpublished) there has been a reduction in photosynthesis and transpiration for a day or so after spray applications, and then recovery. However, the data on leafhopper injury presented here show that a leaf does not recover its original status in respect to apparent photosynthesis once it has been even moderately injured. This fact is of special importance where early season leafhopper injury occurs on leaves. Cell structure and the capacity of the leaf to function properly are adversely affected for the remainder of the season. This emphasizes the importance of early control of leafhoppers, both from the standpoint of reducing later populations of the insects and of obviating the permanent effects that they may have on leaf metabolism.

SUMMARY AND CONCLUSIONS

Injury to Stayman Winesap apple leaves caused by several species of apple leafhoppers (*Typhlocyba* spp.), grape leafhoppers (*Erythroneura* spp.), and the potato leafhopper (*Empoasca fabae*) was accompanied by a more or less marked reduction in apparent photosynthesis and transpiration. Photosynthesis usually was affected sooner and to a greater extent than transpiration.

A given number of potato leafhoppers had a more detrimental effect on leaf metabolism than an equal number of apple or grape leafhoppers.

Cross sections of injured leaves showed that the mesophyll-feeding types of leafhopper (*Typhlocyba* spp. and *Erythroneura* spp.) removed the contents of the cells in the palisade layers, while the spongy mesophyll cells were not significantly affected unless the leaf had been severely injured.

The data show that apparent photosynthesis and transpiration of apple leaves may be reduced early in the growing season when the leafhopper population is moderately low, and when this occurs the capacity of the injured leaves to function normally is permanently impaired. Early control of these insects is therefore important.

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EFFECT OF EROSION ON FERTILITY CHANGES IN THE SHELBY LOAM PROFILE [1]

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INTRODUCTION

It is generally accepted that under virgin conditions the soil is never completely depleted of its fertility, but tends to reach a level of fertility in equilibrium with that of its environment (*1*).[3] The supply of nutrients is adequate, therefore, for the native vegetation. Soil-fertility-depleting factors, such as cultivation, are absent. Erosion is at a minimum.

The effects of most farming operations, with the commonly attendant removal of soil by erosion, have in too many instances decreased the once relatively large amount of nutrients in the soil. Observations suggest, also, that all too often farmers have used management practices that they believed would maintain or increase the productivity of their soil, when such practices were failing to achieve this purpose.

Data obtained at the Soil Conservation Experiment Station, Bethany, Mo., show that, under similar conditions of soil, slope, and climate, the rate of soil removal is dependent largely upon the crop and cultural treatment.[4] Each treatment affords its own degree of protection against the erosional action of water. Crop and management practices also cause chemical, physical, and biological effects on the soil that change the original soil properties.

Accurate soil- and water-loss records from several plots have been kept at the Bethany station for a number of years. Soil-fertility analyses of these data have been made to learn how soil- and crop-management practices may affect soil losses or losses and gains in soil fertility. The results of these preliminary studies dealing with soil and water losses under different crop and cultural treatments are presented here, as such losses reflect the changes in fertility brought about by them.

PLAN OF STUDY

Soil samples were taken from plots of series 1 of the Bethany station, which are maintained for comparative studies of various soil- and crop-management practices. The cropping system, soil and water losses, and other pertinent data are given in table 1. The plots were prepared in 1930, and the records for a complete crop year were begun on January 1, 1931, so that effects during 7 years have been measured.

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TABLE 1.—*Average annual soil and water losses for a 7-year period (1931–37), Shelby silt loam, plot series 1, Bethany, Mo.*

Plot No.[1]	Crop	Precipitation	Surface run-off			Soil loss, run-off per acre		Period required for 7-inch surface erosion [2]
			Quantity	Percentage of precipitation	Density per acre-inch			
		Inches	*Inches*	*Percent*	*Tons*	*Tons*	*Inches*	*Years*
1	Corn, annually	31.45	9.07	28.84	7.32	66.35	0.44	15.1
2	do	31.45	9.15	29.09	5.80	53.03	.35	18.9
3, 4, 5	Rotation untreated [3]	31.45	5.11	16.25	1.72	8.81	.06	113.5
5	do [3]	31.45	4.98	15.83	1.04	5.18	.04	
6	Rotation, fertilized [4]	31.45	3.96	12.59	.93	3.69	.03	
7	Alfalfa, fertilized [5]	31.45	2.50	7.95	.08	.20	.001	5,000
8	Bluegrass	31.45	3.06	9.73	.07	.22	.001	4,545
9	Surface fallow	31.45	9.28	29.51	9.28	86.15	.58	11.6
10	Subsoil fallow [6]	31.45	9.32	29.63	6.46	60.25	.40	16.6

[1] Plot 1, length, 145.2 feet; 0.02 acre. Other plots, length, 72.6 feet; 0.01 acre. All plots, width, 6.0 feet; slope, 8 percent.
[2] Weight of plow-depth soil taken as 2 million pounds per acre.
[3] Rotation: Corn, wheat (clover-timothy), clover-timothy.
[4] Lime, 3 tons per acre, 1930; 20-percent superphosphate, 250 pounds per acre on wheat. Rotation: Corn, wheat (clover-timothy), clover-timothy.
[5] Lime, 3 tons per acre, 1930; 20-percent superphosphate, 250 pounds per acre, every 3 years.
[6] In 1930, 7 inches of surface soil removed.

In order that the changes in fertility through the removal of soil by erosion from the different plots under various crop and cultural treatments might be compared on some basis, the study included an analysis, obtained in 1939 from a plot continuously in bluegrass since 1930, of 1-inch horizons of a 0- to 13-inch profile. Since the amount of soil lost from this plot has been negligible during the time of the experiment, and since this plot simulates virgin conditions, it was taken as a basis for comparing the amount of soil lost and for evaluating the gain or loss in fertility of the other plots. Comparisons could be made of the 0- to 7-inch horizon of any plot according as it corresponded to 7 successive 1-inch horizons of the 0- to 13-inch profile.

Originally all the plots had the same depth of surface soil, and therefore the equivalent horizons of plots for comparing with the continuous bluegrass plot could be obtained by taking into consideration the amount of surface soil, in inches, that had been removed by erosion. A 13-inch depth was chosen arbitrarily as sufficient, because this depth extended into the subsoil or B horizon of the Shelby soil, and because soil removal on none of the plots had exceeded this depth. In general, this method of approach conforms to the practice followed in making conservation surveys (*8*). Characteristics of profiles undisturbed by erosion were used as a basis from which to determine the degree of erosion that had occurred on truncated soil profiles.

Another reason for extending the sampling to include part of the subsoil is the fact, brought out by conservation surveys, that many of the Shelby soil areas now are being farmed on or near subsoil levels. Additional information is needed in order to treat the subject of subsoil farming more intelligently. Soil- and crop-management practices advocated for comparatively noneroded soils apparently have not met with success when applied indiscriminately to more or less desurfaced soils.

Further information pertaining to the plots is contained in a report from the Bethany [5] station, and various chemical and physical characteristics of the Shelby loam profile and the soil on each plot are reported in other publications of the Department of Agriculture (*6, 7, 10*).

Annual samples, representing a composite of seven borings for each plot, taken by beginning 5 feet from the top of the slope and extending downward at 10-foot intervals, were obtained each fall from the surface 7-inch layer of the plots under study. Plot 1, in continuous corn, was twice the length of the other plots, and was divided equally into upper and lower sections. Each section was sampled like the other plots. Plot 8, in continuous bluegrass, which was used as the basis for comparisons with the other plots, was sampled during the spring of 1939 by 1-inch horizons to a 13-inch depth. The seven borings on this plot for each 1-inch horizon were composited. These samples of limited horizons measure the changes by 1-inch surface units that would occur in the profile with progressive erosion.

To obtain a measure of the changes in fertility of the plots, the successive 1-inch profile samples (0 to 13 inches) taken on plot 8, in 1939, and the annual composite surface samples (0 to 7 inches) taken in 1931, 1933, 1935, and 1937 on the other plots, were analyzed for their total exchange capacity, exchangeable calcium, exchangeable magnesium, total carbon content, total nitrogen content, and hydrogen-ion concentration. Ammonium acetate was used as the leaching agent for the base-exchange determinations. Exchangeable calcium and magnesium in the leachate were determined by standard analytical methods. The total carbon content was measured by dry combustion and converted to organic-matter percentages by using the conventional Wolff factor, 1.724. The Kjeldahl method was used in determining total nitrogen. The pH was measured with a quinhydrone electrode.

EXPERIMENTAL RESULTS

The results may be shown most conveniently by presenting first the data from the profile of plot 8, continuously in bluegrass and with insignificant erosion. The properties of the successive 1-inch horizons of this noneroded profile will serve as a basis for comparing the properties of the profiles of the other plots under their different treatments. Any differences will correspond to greater or lesser amounts of erosion and truncation of the profiles of these plots.

PROFILE CHARACTERISTICS OF THE NONERODED SOIL

Characteristics determined for the 1-inch horizons for the 0- to 13-inch profile on the noneroded bluegrass plot (plot 8) included total exchange capacity, exchangeable calcium, exchangeable magnesium, pH, organic matter, and nitrogen. The detailed data are given in table 2 and presented graphically in figures 1 and 2. Perhaps the most noticeable fact in the data, considered as a whole, is the similarity in properties of the first six or seven successive 1-inch horizons.

[5] See footnote 4.

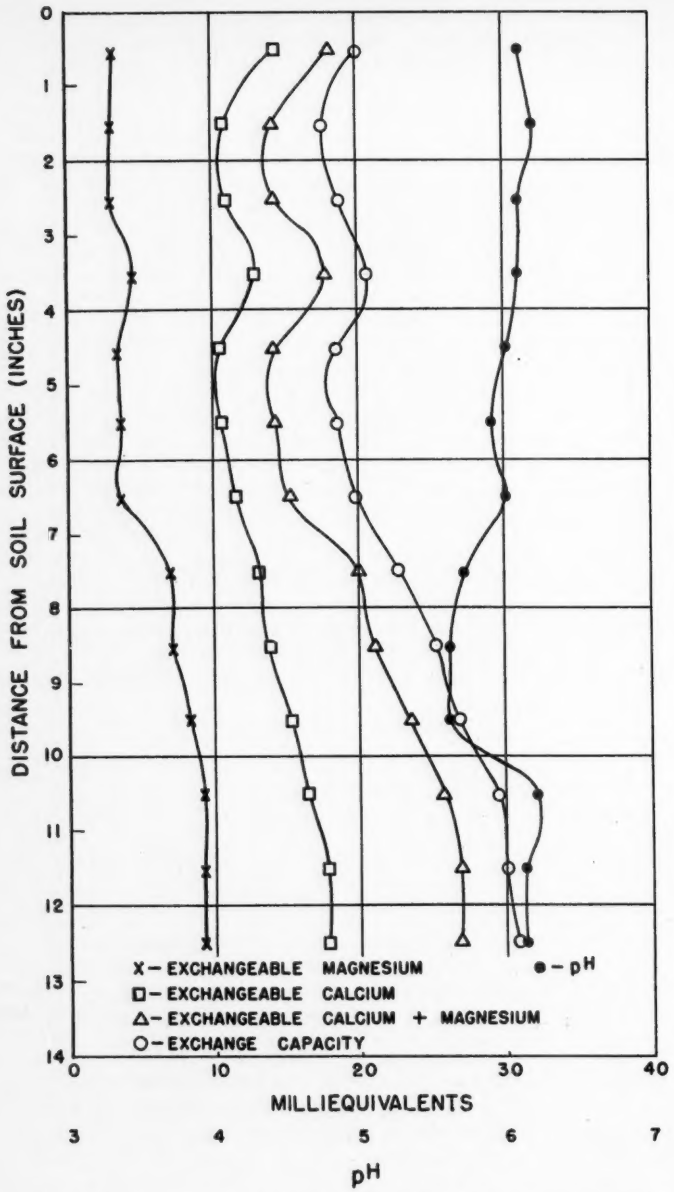

FIGURE 1.—Exchangeable calcium and magnesium, total exchange capacity, and of the soil at different levels in the profile of the noneroded bluegrass plot.

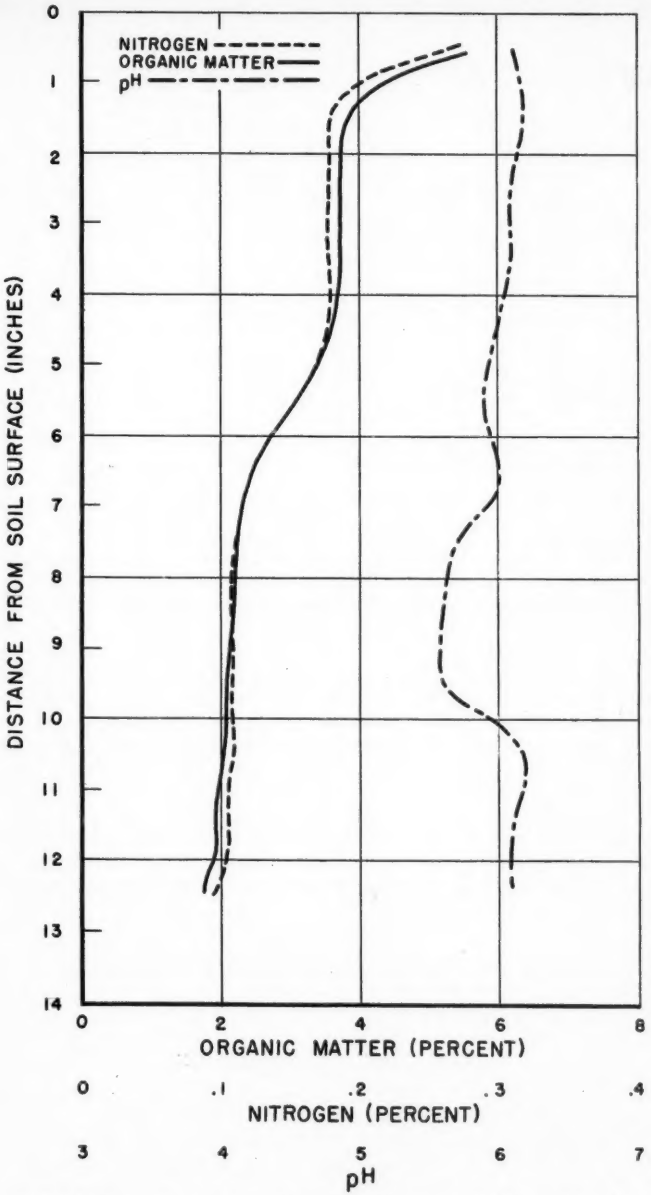

FIGURE 2.—Nitrogen, organic matter, and pH of soil at different levels in the profile of the noneroded bluegrass plot.

TABLE 2.—*Chemical properties of bluegrass plot profile, 1939, Shelby silt loam*

Profile depth (inches)	Total exchange capacity	Exchangeable calcium		Exchangeable magnesium		Total exchangeable calcium-magnesium		Organic matter	Nitrogen	C/N ratio	pH
	Milliequivalents [1]	*Milliequivalents* [1]	*Percent* [2]	*Milliequivalents* [1]	*Percent* [2]	*Milliequivalents* [1]	*Percent* [2]	*Percent*	*Percent*		
0–1	20.10	14.60	72.64	3.68	18.31	18.28	90.95	5.71	0.270	12.28	6.1
1–2	17.80	10.93	61.40	3.37	18.93	14.30	80.34	3.82	.181	12.24	6.2
2–3	18.77	11.02	58.71	3.34	17.79	14.36	76.51	3.75	.179	12.14	6.1
3–4	20.65	12.98	62.86	4.75	23.00	17.73	85.86	3.71	.178	12.08	6.1
4–5	18.48	10.63	57.52	3.59	19.43	14.22	76.95	3.61	.177	11.84	6.0
5–6	18.53	10.56	56.99	3.72	20.08	14.28	77.06	3.09	.154	11.66	5.9
6–7	19.84	11.50	57.96	3.69	18.60	15.19	76.56	2.44	.121	11.67	6.0
7–8	22.54	12.94	57.41	7.00	31.06	19.94	88.46	2.29	.111	11.99	5.7
8–9	25.00	13.79	55.16	7.12	28.48	20.91	83.64	2.19	.110	11.53	5.6
9–10	26.49	15.04	56.78	8.31	31.37	23.35	88.15	2.10	.108	11.29	5.6
10–11	29.22	16.32	55.85	9.13	31.25	25.45	87.10	2.05	.107	11.14	6.2
11–12	29.73	17.57	59.10	9.04	30.41	26.61	89.51	1.94	.105	10.72	6.1
12–13	30.66	17.48	57.01	9.10	29.68	26.58	86.69	1.78	.097	10.66	6.1
0–7	19.17	11.75	61.29	3.73	19.46	15.48	80.75	3.73	.180	12.03	6.1
7–13	27.27	15.52	56.91	8.28	30.36	23.81	87.31	2.06	.106	11.26	5.9
0–13	22.91	13.49	58.88	5.83	25.45	19.32	84.33	2.96	.146	11.75	6.0

[1] Milliequivalents per 100 gm. of soil.
[2] Percentage of total exchange capacity.

TOTAL EXCHANGE CAPACITY, EXCHANGEABLE CALCIUM, AND EXCHANGEABLE MAGNESIUM

The total exchange capacity, exchangeable calcium, and exchangeable magnesium were fairly constant in the surface 7 inches of soil. This is due partly to the effect of soil mixing resulting from plowing prior to the time when the bluegrass was established on the plot. No explanation can be given at the present time for the increase in the 3- to 4-inch layer. The effect of organic matter on the base-exchange properties is shown in the 0- to 1-inch horizon. This horizon has a higher organic-matter content (5.71 percent), with a correspondingly higher amount of exchangeable calcium (14.60 milliequivalents per 100 gm. of soil) than the average organic-matter content (3.73 percent) and exchangeable calcium (11.75 milliequivalents) for the 0 to 7-inch horizon. The total exchange capacity and exchangeable magnesium increased less, proportionately, in the corresponding horizons. A gradual increase in magnitude occurred as the clay content increased with depth. Base saturation followed the same trend.

pH VALUES

The pH values of the soil were fairly constant in the surface 7 inches. They decreased in the 7- to 10-inch horizons, and increased in the lower 3 inches to approximately the values of the surface 7 inches.

ORGANIC MATTER AND NITROGEN

The organic matter and the nitrogen content both decreased decidedly at approximately the 6-inch level in the profile. An independent study of the depth of root penetration of different crops tested at the station showed that the mass of bluegrass roots did not penetrate much below 6 inches. This fact and the prior effects of plowing may account for the change.

The progressive accumulation of organic matter in the continuous bluegrass plot for the period 1931 to 1937 (table 3, plot 8), and the

TABLE 3.—*Chemical properties of plots of series 1, Shelby silt loam*

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Plot No. and treatment	Year	Total exchange capacity	Exchangeable calcium		Exchangeable magnesium		Total exchangeable calcium and magnesium		Organic matter	Nitrogen	C/N ratio	pH
		Milliequivalents [1]	*Milliequivalents* [1]	*Percent* [2]	*Milliequivalents* [1]	*Percent* [2]	*Milliequivalents* [1]	*Percent* [2]	*Percent*	*Percent*		
1-U; corn annually	1931	19.61	12.03	61.35	3.85	19.63	15.88	80.98	4.05	0.194	12.13	5.7
	1933	18.85	12.28	65.15	4.17	22.12	16.45	87.27	3.64	.178	11.86	6.1
	1935	19.27	11.99	62.22	3.92	20.34	15.91	82.56	3.65	.180	11.77	6.2
	1937	18.38	10.95	59.58	3.41	18.55	14.36	78.13	3.44	.160	12.46	5.6
1-L; corn annually	1931	16.80	10.61	63.16	3.41	20.30	14.02	83.45	3.21	.151	12.35	6.2
	1933	17.34	11.61	66.96	3.78	21.80	15.39	88.75	3.01	.145	12.04	6.1
	1935	17.24	10.66	61.83	4.01	23.26	14.67	85.09	2.50	.127	11.42	6.2
	1937	18.94	10.31	54.44	3.81	20.12	14.12	74.55	2.38	.116	11.90	6.1
2; corn annually	1931	17.09	9.97	58.34	3.45	20.19	13.42	78.53	2.93	.146	11.63	5.8
	1933	17.04	10.35	60.74	3.69	21.65	14.04	82.39	3.03	.147	11.98	6.1
	1935	16.62	9.43	56.74	3.59	21.60	13.02	78.34	2.64	.129	11.89	6.0
	1937	19.08	10.05	52.67	3.88	20.34	13.93	73.01	2.49	.125	11.53	6.2
3; rotation, untreated [3]	1931	17.39	10.92	62.79	3.66	21.05	14.58	83.84	3.47	.164	12.26	5.9
	1933	17.60	10.77	61.19	3.30	18.75	14.07	79.94	3.30	.168	11.38	5.8
	1935	17.03	9.31	54.67	3.46	20.32	12.77	74.99	3.20	.157	11.81	5.8
	1937	18.32	9.57	52.24	3.45	18.83	13.02	71.07	3.08	.161	11.08	5.8
4; rotation, untreated [3]	1931	17.45	10.02	57.42	3.70	21.20	13.72	78.62	3.50	.169	12.03	5.6
	1933	17.55	9.84	56.07	3.27	18.63	13.11	74.70	3.56	.175	11.79	5.6
	1935	16.89	10.07	59.62	3.63	21.49	13.70	81.11	3.34	.170	11.40	5.4
	1937	18.32	10.06	54.91	3.48	19.00	13.54	73.91	3.43	.164	12.12	5.8
5; rotation, untreated [3]	1931	19.94	13.22	66.30	3.54	17.75	16.76	84.05	3.61	.172	12.15	5.7
	1933	18.35	10.66	58.09	2.97	16.19	13.63	74.28	3.59	.183	11.40	5.5
	1935	18.05	10.58	58.58	3.40	18.83	13.98	77.41	3.47	.175	11.49	5.5
	1937	17.98	10.17	56.56	3.46	19.24	13.63	75.81	3.38	.163	12.03	6.1
6; rotation, fertilized [4]	1931	18.75	11.38	60.69	3.65	19.47	15.03	80.16	3.33	.164	11.77	5.7
	1933	18.29	12.83	70.49	3.16	17.36	15.99	87.86	3.65	.178	11.89	6.8
	1935	19.05	15.34	80.52	3.76	19.74	19.10	100.26	3.57	.175	11.82	6.1
	1937	19.27	14.38	74.62	3.29	17.07	17.67	91.70	3.57	.167	12.40	6.1
7; alfalfa, fertilized [5]	1931	18.95	11.01	58.10	4.01	21.16	15.02	79.26	3.79	.184	11.96	5.5
	1933	19.17	12.42	64.79	3.27	17.06	15.69	81.85	3.91	.186	12.18	6.9
	1935	20.02	17.56	87.71	3.47	17.33	21.03	105.04	4.05	.196	11.98	6.5
	1937	19.72	15.25	77.33	3.32	16.84	18.57	94.17	4.02	.192	12.15	6.3
8; bluegrass	1931	19.98	11.32	56.66	4.12	20.62	15.44	77.28	3.53	.173	11.85	5.6
	1933	19.06	10.50	55.09	3.88	20.36	14.38	75.45	3.71	.185	11.63	6.3
	1935	19.20	13.42	69.90	3.98	20.73	17.40	90.63	4.07	.190	12.41	6.2
	1937	19.35	13.73	70.96	3.85	19.90	17.58	90.85	4.29	.205	12.15	6.2
9; surface fallow	1931	20.01	11.42	57.07	3.97	19.84	15.39	76.91	3.43	.163	12.21	5.5
	1933	21.86	11.89	54.39	4.71	21.55	16.60	75.94	2.74	.137	11.61	6.3
	1935	21.40	11.98	55.98	4.99	23.32	16.97	79.30	2.61	.132	11.45	5.4
	1937	24.09	13.40	55.62	5.63	23.37	19.03	79.00	2.38	.122	11.33	5.7
10; subsoil fallow [6]	1931	26.63	17.42	65.41	5.06	19.00	22.98	86.29	2.06	.102	11.70	6.0
	1933	27.64	16.47	59.59	7.39	26.74	23.86	86.32	1.95	.091	12.42	6.0
	1935	26.23	16.44	62.68	7.65	29.17	24.09	91.84	1.94	.085	13.20	5.9
	1937	28.37	17.12	60.35	8.44	29.75	25.56	90.10	1.59	.084	10.97	5.7

[1] Milliequivalents per 100 gm. of soil. [2] Percentage of total exchange capacity. [3] Rotation: Corn; wheat (clover-timothy); clover-timothy.
[4] Lime, 3 tons per acre, 1930; 20-percent superphosphate, 250 pounds per acre on wheat. Rotation: Corn; wheat (clover-timothy); clover-timothy.
[5] Lime, 3 tons per acre, 1930; 20-percent superphosphate, 250 pounds per acre every 3 years. [6] In 1930, 7 inches of surface soil removed.

high base saturation of the exchange complex suggest that the calcification process of soil development might be operating under these environmental conditions. There may have been considerable leaching, but even so it was not enough to remove much of the carbonates to lower levels in the profile.

The process of leaching may have been retarded during this period especially during the last 2 years, a fact which might be attributable to the precipitation deficiency of 22 inches for the 7-year period. The normal annual precipitation, based on 50 years of records, obtained at the United States Weather Bureau Station at Bethany, is 34.44 inches. In 1936 and 1937 the annual precipitation was only 24.43 and 21.80 inches respectively.

The accompanying increase in nitrogen content suggests that conditions may have been favoring increased microbial activity of nonsymbiotic nitrogen-fixing organisms. Definite conclusions on this point, however, are not warranted at this time, nor will they be until the microbial relationship of these plots is studied.

Albrecht and Smith (*2*) have shown that for the nonlegumes redtop and bluegrass, a soil completely saturated with calcium was more effective in the delivery of nitrogen from the supply in the soil to the crop than was a partly saturated soil. Since the percent base saturation for this plot (plot 8, table 3) increased from 77 in 1931 to 91 in 1937, and since environmental conditions suggest a minimum leaching of nitrogen, it appears that the relatively large increase in nitrogen found for the continuous bluegrass plot is not entirely fortuitous. It would seem that the nitrogen accretion can be attributed at least in part to an accumulation of the immobile nitrogen combined in the residue of plant and microbiological tissues.

Recent work has shown that nitrogen moves downward more rapidly in acid than in alkaline soil profiles (*9*); lime also has been found to flocculate a part of the organic nitrogen in solution. It appears that when there was a change in soil reaction from moderate acidity (pH 5.6) to nearer neutrality (pH 6.2), accompanied by a 25-percent increase in the calcium saturation of the exchange complex, the rate of nitrogen removal to lower horizons was reduced. The result was an increase in nitrogen content from 0.173 in 1931 to 0.205 percent in 1937.

The accumulation of organic matter has not only increased the nitrogen content, but its subsequent decomposition has set free all the other nutrients found in combination with it. Greater quantities of organic acids are released by the greater amount of decomposing organic matter. These, in turn, release greater stores of mineral nutrients, such as calcium, from the soil minerals. These combined effects, along with the increased microbiological activity, may explain in part the progressively larger amounts of exchangeable bases found under continuous bluegrass.

PROFILE CHARACTERISTICS OF THE ERODED SOILS

That truncation of a profile by erosion reduces the fertility content in measurable amounts is indicated by comparing the characteristics of the eroded plots with those of the noneroded profile under bluegrass. Plowing and cultivation of the surface soil, which bring up soil from deeper horizons, serve to complicate the measurement of the changes in the surface-soil characters caused by erosion. Observation and

evaluation of these disturbances in the profile are possible from the station studies.

Total Exchange Capacity

An excessive soil loss from the Shelby loam is reflected in an increase in the total exchange capacity of the remaining exposed surface. This is demonstrated clearly by the data in table 3 for plots 2 and 9, on which excessive erosion occurred, and by plot 10, which was artificially eroded by removing 7 inches of surface soil in 1930. By calculating the soil loss in tons per acre on the acre-inch basis and using this figure to determine the amount of surface soil removed, it is evident that progressive amounts of the subsoil became mixed with the surface soil each year in which it was tilled to a constant depth for the following crop. Physical analyses of a typical profile from these plots show that the clay content increased with depth (*6*). As the progressive mixing of the surface and subsoil continued, the total exchange capacity increased, since clay content and total exchange capacity are closely associated.

Although plot 1 cannot be compared directly with the other plots, because it is twice their length, the data in table 3 show that as erosion increased, the exchange capacity decreased in the upper half and increased in the lower half of the plot. It is known that, as the length of slope increases for this type of soil (*12*),[6] the amount of soil lost increases. This increase was greater on the lower half of the plot, where more of the subsoil was eroded. The upper half of the plot shows the effect that organic matter has on total exchange capacity. As the organic matter decreased, the exchange capacity also decreased. With but a small soil loss, and with the organic matter remaining constant (plots 3, 4, 5) or increasing (plots 6, 7, 8), the total exchange capacity remained at approximately the same level for the 7-year period.

Exchangeable Calcium and Magnesium

An examination of the data for plots 1, 2, 9, and 10 in table 3 shows that a general parallelism exists between the exchangeable bases and the clay content. In these plots erosion has removed various amounts of surface soil, and this should, according to determinations of the profile reported elsewhere (*6*), result in the incorporation of increasing amounts of clay from the subsoil into the surface soil. Since these plots (1 and 2, continuous corn; 9 and 10, fallow) received only small increments of organic matter or none, the effect of organic matter on the exchangeable bases is minimized. This is clearly shown by plot 2, where, as the percentage of organic matter decreased, an increase in clay content counteracted the decrease to maintain an approximately constant level of exchangeable bases.

The effect of organic matter on exchangeable calcium also is demonstrated. Where the amount of soil eroded was small, but an increase (plot 8) or decrease (plots 3, 4, 5) in organic matter had occurred for the period, there were corresponding increases or decreases in exchangeable calcium. As was to be expected for plots 6 and 7, fertilizer and limestone treatments materially increased the milliequivalents of exchangeable calcium.

[6] See footnote 4.

pH Values

There was no direct relationship between pH and rate of soil loss. There appeared to be no relationship between pH and exchange capacity, or exchangeable calcium and magnesium; McGeorge (*5*) previously reported a similar lack of relationship.

Organic Matter and Nitrogen

There appears to be a relationship between surface-soil removal and the percentage of organic matter and total nitrogen content in the remaining soil (table 3). In the continuous bluegrass plot there was a progressive increase of organic matter and nitrogen and a negligible loss of soil, in contrast to a progressive decrease of organic matter and nitrogen with high soil losses in the fallow and continuous corn plots.

Comparison of the nitrogen content of the continuous bluegrass plot with that of the rotation plots (plots 3, 4, 5, 6) shows that the latter did not reach the nitrogen level attained by the bluegrass plot. This observation agrees with that of Jenny (*4*) on the effect of farming operations on the nitrogen content of the soil.

When the data for the untreated rotation plots 3, 4, and 5 are averaged by years it is found that this rotation did not maintain the original level of organic matter and nitrogen. Some idea of the effect that soil treatment may have can be obtained by comparing plot 6 (treated) with plot 5 (untreated). Although the original level of nitrogen and organic matter was lower on plot 6, the values in table 3 show that on this plot (rotation with soil treatment) the organic matter and nitrogen content were maintained, while on plot 5 (rotation without soil treatment) both decreased slightly. The treated rotation not only maintained the organic matter and nitrogen, but operated also to decrease the soil loss.

DISCUSSION AND CONCLUSIONS

Soil surveyors know that it is often difficult to ascertain how much of the original surface soil has been removed by erosion. This is true especially where the surface soil has been mixed with the underlying subsoil by plowing. With the plots studied, all having had different rates of losses, depending upon the crop and cultural treatment, some understanding of the relative position of each plot with regard to native profile conditions may be obtained by comparison with the 0-to-13-inch standard profile.

In order to compare the data from other plots with the profile of plot 8 (continuous bluegrass), it was necessary to plot the magnitude of the soil property under consideration against soil loss. Since soil loss from plot 8 was negligible, and since the annual composite samples were taken from the top 7 inches, the average of the top seven 1-inch horizons of this plot was taken as zero soil loss. This procedure is logical, since originally all plots had the same soil depth, except plot 10 which was desurfaced.

Two lines are plotted in figures 3 and 4 from the data for plot 8. Both lines are made of data secured from the analysis of samples collected in 1939, but corrected for each 1-inch horizon, to such extent as the average of the seven 1-inch horizons in 1939 varied from the value of the single 7-inch sample in 1931. No samplings other than those of 7-inch horizons previously had been made. While this

method of correction may be open to criticism, it was taken as the best at hand for comparative purposes.

The broken line in figures 3 and 4 results when it is assumed that successive 1-inch layers of soil are lost from the surface, which would

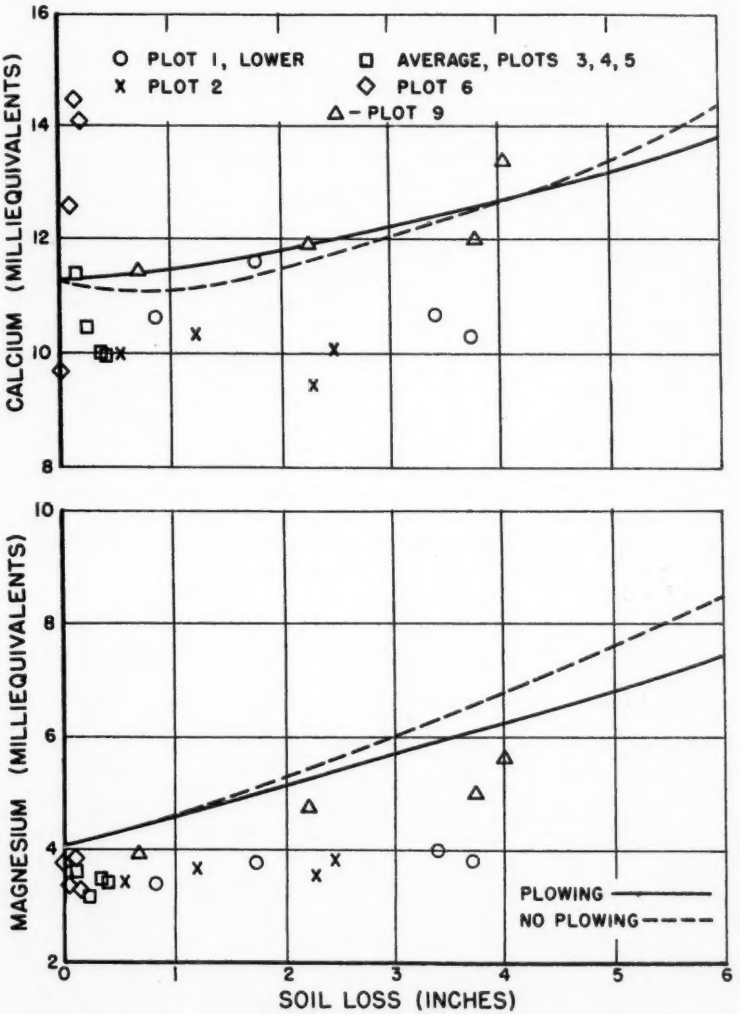

FIGURE 3.—Changes in exchangeable calcium and magnesium in the surface soil with erosion, without plowing and with plowing to a depth of 7 inches.

be the case without plowing. This loss amounts to a running average of 7 inches, using the data in table 2. The solid line represents the results obtained when plowing to a depth of 7 inches is assumed each time 1 inch of soil is lost. By the use of this last method an attempt

is made to consider the mixing effects resulting from tilling the soil for cultivated crops.

No attempt was made to compare directly the plots in series 1 with selected 1-inch horizons of the continuous bluegrass plot; emphasis

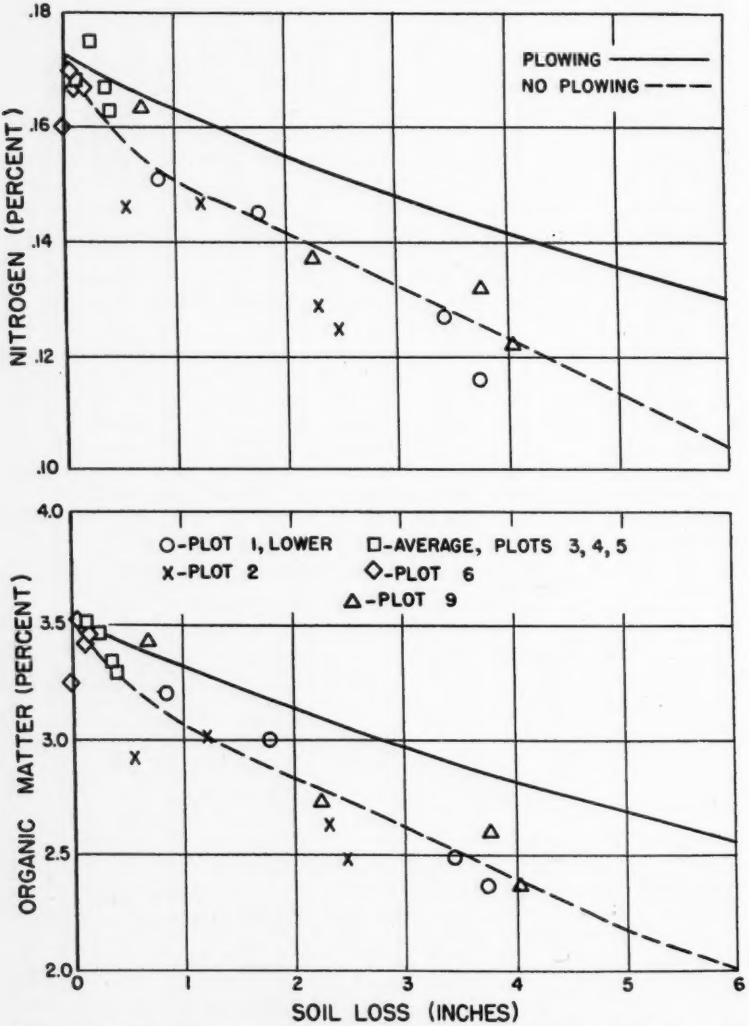

FIGURE 4.—Changes in organic matter and nitrogen in the surface soil with erosion, without plowing and with plowing to a depth of 7 inches.

was placed rather on observing the trend of the values in these plots and comparing them with the values obtained for the continuous bluegrass plot.

Figure 3 illustrates the fact that when 1 inch of topsoil is removed

by erosion, it does not necessarily follow that the exchangeable calcium and exchangeable magnesium in the remaining soil profile will conform to that of the respective horizons contained under native profile conditions (0- to 13-inch profile). However, the plotted results show that with progressive accumulative erosion losses, which means that the profile will be truncated more each year, the soil properties tend to follow the design of the values obtained for the native profile. For the Shelby loam, the results show that as depth increases, the total exchange capacity and exchangeable bases increase. Slater and Byers (*10*) reported similar results for the exchangeable bases of the soil colloids by definite horizon depths for this soil profile.

From figure 4 it would seem that the organic-matter and nitrogen content change at very nearly the rate indicated by plot 8, when no plowing is assumed (broken line). But since all plots except 8 were tilled—plots 1, 2, and 9 annually and 3, 4, 5, and 6 every 3 years—they might be expected to follow the solid line (plowing). The fact that decreases in organic matter and nitrogen are greater than would be expected may be explained by the fact that the line plotted for plot 8 takes into account only the losses subsequent to erosion, and not those that accompany crop production and oxidation brought about by plowing.

Slater and Carleton (*11*) reported earlier on the loss of soil organic matter in this region. They found that organic-matter content dropped 0.002 percent on both Shelby and Marshall soils for each ton of soil lost by erosion. This value was calculated by assuming a linear regression, and they point out that "the line in reality must be a curve since the organic-matter content of the soil cannot be reduced below zero, while erosion can continue indefinitely."

The results of this study indicate that the rate of loss of organic matter and nitrogen decreases, which also gives a curved line. Albrecht (*1*) points out that—

> this high rate of depletion will not continue. As is true for all biochemical processes, the early rate of consumption is rapid, which gives a sudden decrease. * * * Long continued experiments, accompanied by soil analyses, prove that the organic-matter content of a soil will reach a fixed level characteristic of the surrounding climatic conditions.

To climatic conditions may be added cropping practices. The bluegrass and alfalfa plots are somewhat above the natural equilibrium in organic-matter content (3.54 percent) for this section of Missouri (*1*); a fertilized rotation of corn, wheat, clover with timothy is approximately in equilibrium; and the same rotation unfertilized is slightly below. It would seem that the plots in corn and fallow have passed the period of sharp decline, and now are decreasing in organic-matter content at a slower rate.

It is of interest to note that, for a 3-year rotation of corn, wheat, and clover-timothy with fertilizer and lime treatment, the fertility of the soil was not only maintained but the yields were increased. Yield-data records for the period show increases of 45 percent for clover-timothy, 69 percent for wheat, but no significant difference for corn as compared with the nontreated plot. Observations suggest that a drought which occurred at a critical period when the corn was maturing had a greater effect on yield than any other single factor.

The results obtained do not indicate that any one soil property can be used as a criterion to evaluate the amount of soil loss, or more

specifically, the amount of surface soil remaining. However, by considering several soil properties it would seem that an evaluation can be made. Of the soil properties studied, organic-matter and nitrogen content appear to indicate most nearly the degree of truncation of soil profiles by erosion.

Values obtained from a study of the 0- to 13-inch horizon indicate that, if the rate of erosion is small, the amounts of subsoil brought to the surface by successive truncations of the profile by erosion will be of benefit to the surface horizon. Exchangeable calcium and magnesium lost through leaching, crop removal, and erosion would be replenished partly or wholly. Nitrogen and organic-matter deficiencies would be corrected by the combined activities of micro-organisms and legumes, since conditions for their growth and development would be favorable. The use of lime and phosphate would still be desirable for maximum yields.

From the recent work of Graham (*3*) it would seem that the average soil loss of 0.025 acre-inch per year from plot 6 would not be so great that the primary minerals incorporated from the subsoil with the surface soil would lower the soil-fertility level. Mineralogical analyses show that this soil contains appreciable amounts of calcium-bearing minerals.[7] Middleton et al. (*6*) found that the percentage of CaO increased with an increase in profile depth.

Unpublished data by Woodruff and Simerly[8] show that under field conditions sand and silt may accumulate as a result of the clay fraction being carried off in suspension by the run-off water. Data reported by Middleton et al. (*7*) for the years 1931 and 1932 for these plots are in agreement with the foregoing conclusions; there is a marked increase in clay content in the soil eroded from the plots as compared with the plot composites.

For the plots fallowed and for those in cultivated crops the mechanical composition of the eroded material is similar to that of the soil remaining. For the uncultivated crops the eroded material is finer in texture than is the surface 7 inches of soil. Therefore, the texture of the soil should not change materially from the original by additions of clay from the subsoil.

The data in table 1 show that a rotation not only keeps the soil loss at a practical minimum, but also greatly reduces surface run-off, as compared with the continuous corn crop. Unpublished results of a study of the relation between precipitation and surface run-off for these plots for a 9-year period (1931–39) show that bluegrass was three times as effective and a rotation of corn, wheat, clover-timothy twice as effective as continuous corn in preventing run-off.[9]

As the cultural operations were with the slope, it appears logical to conclude that if these operations were carried out on the contour, the soil and water losses would be reduced further. Data from experimental area 5–N, which is similar to the fertilized rotation plot in soil type, slope, and treatment, except that it represents a field actually terraced and contour cultivated, show that the soil loss for a 6-year period (1932–37) was 1.02 tons per acre per year. At this

[7] Unpublished soil mineralogical data, by J. R. Johnson. Iowa Agr. Expt. Sta. 1939.

[8] WOODRUFF, C. M., and SIMERLY, M. E. THE SIZE DISTRIBUTION OF MATERIALS ERODED FROM DIFFERENT SLOPES. Unpublished data. Mo. Agr. Expt. Sta. 1940.

[9] SMITH, D. D., and SWANSON, C. L. W. A PRELIMINARY STUDY OF THE RELATIONSHIP BETWEEN PRECIPITATION AND SURFACE RUN-OFF. Unpublished data. U. S. Soil Conserv. Serv. Res., Conserv. Expt. Sta., Columbus, Mo. 1940.

rate of soil loss, 980 years would be required to remove the surface 7 inches.

These data also suggest that the application of conservation measures on a practical field basis to reduce the deleterious effects of erosion would not only reduce to a practical minimum soil and water losses, but would also maintain the fertility of the soil.

It appears possible that soil of types similar to Shelby loam can be rejuvenated and conserved for years to come. The data obtained seem to suggest that there is some benefit to be gained by the addition of small increments of subsoil to the surface soil, if at a slow enough rate and when combined with the organic matter introduced by proper cropping. This result may be achieved by employing judicious soil-, crop-, and conservation-management practices.

SUMMARY

Data are presented showing the results of analyses for total exchange capacity, exchangeable calcium, exchangeable magnesium, organic-matter content, nitrogen content, and hydrogen-ion concentration of Shelby loam from plots planted to different crops and maintained under different cultural conditions at the Soil Conservation Experiment Station, Bethany, Mo. Results of the same determinations on 1-inch horizons of a 0 to 13-inch profile continuously in bluegrass also are reported for comparative purposes.

According to the data for the profiles by 1-inch horizons, the exchange capacity, the exchangeable bases, and the base saturation increase whereas the organic matter and nitrogen content decrease with increasing depth.

Nitrogen and organic matter appear to decrease at a decreasing rate as erosion progresses. In general a decrease in organic matter and nitrogen occurred with increased soil loss. This decrease occurred at a rate below that to be expected from the profile study.

The base exchange properties follow the trend of the values for the 0 to 13-inch profile of the bluegrass plot. The effect of organic matter on these properties is pointed out.

It was found that the fertility of the soil was maintained by a 3-year rotation of corn, wheat, clover-timothy with fertilizer and lime treatments. The rate of soil loss was small enough so that the deleterious effects were counteracted by the incorporation of small increments of the subsoil. The clay added from the subsoil was removed in the surface run-off in such amounts as not to alter materially the texture of the soil. Additions of subsoil increased the amounts of exchangeable calcium and magnesium.

No relation was observed between the concentration of hydrogen-ions in the soil and soil loss.

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FACTORS AFFECTING DISTRIBUTION AND SEVERITY OF BLACK ROOT ROT OF APPLE TREES[1]

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INTRODUCTION

Certain aspects of the geographic, ecologic, and host-parasite factors that appear to affect the distribution and severity of black root rot of apple trees, caused by *Xylaria mali* Fromme, and experiments dealing with some physiological studies of the pathogen are reported herein. Since the distribution of this root rot is restricted, a study of its environmental limitations, together with inoculation experiments, should throw some light on the conditions favoring or hindering infection.

DISTRIBUTION AND SEVERITY OF BLACK ROOT ROT

Black root rot is distributed from Pennsylvania to Georgia and westward to Arkansas. Serious losses have been confined to the central and southern parts of the range, and the losses in Pennsylvania and Maryland have been unimportant. The greatest losses have occurred in the fruit-growing sections of Virginia, West Virginia, and the States to the south and also in the Ozark region. Although the root rot has been observed in the Coastal Plain, which is not an extensive fruit-growing section, it has not caused severe losses there. The general distribution of the disease is probably influenced directly or indirectly by temperature. As will later be shown (p. 302), the optimum temperature, about 25° C., for the strain of the pathogen studied is fairly high for a soil-inhabiting organism. Temperature may be a factor in the frequent occurrence of the disease in Virginia and other Southern States and in its infrequent occurrence in Pennsylvania.

High temperature may influence susceptibility by favoring the pathogen or by adversely affecting host resistance.

Even within the range of its most frequent occurrence there is considerable irregularity in the distribution of the disease. No adequate explanation for this can be given at this time. Among the possible contributing factors may be genetic differences in the parasite. A study of the pathogenicity of different isolates, reported elsewhere in this paper (p. 303), gives some ground for this conclusion. Probably the most important factor, however, that affects the local distribution of the disease is the edaphic environment of the host.

Possibly a deficiency of moisture is concerned in the local abundance of the disease. Many instances have been observed in which the disease was much more prevalent on a knoll where moisture and fertility were presumably less favorable to tree growth than in the rest of the orchard. However, consideration should be given the

[1] Received for publication April 22, 1942.

following correspondence from F. J. Schneiderhan, who, with F. D. Fromme, spent several years in intensive work on this disease in the Shenandoah Valley apple section of Virginia:

> I have found more root rot in orchards growing in rich orchard soil than in poor soil. Most of Fromme's and my observations were made in the better orchards in Virginia and West Virginia. I admit that we found considerable mortality on Ben Davis orchards after the 1930 drought, but in most of these cases root rot was associated with blister canker and I do not know which was the major factor. * * *
>
> Some of the severest infections found near Winchester were at the lower part of orchard slopes where moisture content and soil nutrients were highest. I have always believed that the availability of fungus inoculum was the important factor in the localization of infection within an orchard.

The distribution and the severity of the disease are probably dependent on a number of interrelated and concomitant conditions.

INFECTION WITH XYLARIA MALI

MATERIALS AND METHODS

Prior to 1936 inoculation work was conducted at Arlington Experiment Farm, Arlington, Va., on nursery trees 2 to 5 years old. In 1936 and later inoculations were made at the United States Horticultural Station, Beltsville, Md. Natural infection by *Xylaria mali* has not been found in these locations, but experience has shown that apple trees growing in these localities may be fairly readily infected by inoculation with pure cultures of the fungus. Unless otherwise stated, the material and methods used were those described below.

Roots of apple (*Malus pumila* Mill.) trees were inoculated in situ by removing enough soil to expose root tissue; against this was laid a piece of apple twig, about 2 inches long, on which a profuse growth of the fungus had been produced in artificial culture. The soil was replaced after inoculation and not disturbed until records were taken, usually at the end of the growing season. In the inoculations made in 1932 and 1933, a wound was made into the cambium. All subsequent inoculations were made by applying the inoculum to a shallow wound made by scraping with a trowel. Unless otherwise stated, the inoculum was a highly pathogenic clone (No. 57) isolated from an infected apple root from Bluemont, Va., and the field inoculations were made in July.

Where inoculations were made on trees that had been dug, the inoculum was held by a rubber band against an open incision in the root and after inoculation the roots were wrapped in paper and stored in moist peat.

Since infection did not occur on uninoculated trees or even on uninoculated portions of inoculated roots, it was not considered necessary to leave part of each plot uninoculated as a check on infection.

EFFECT OF KIND AND QUALITY OF INOCULUM

On February 2, 1934, inoculations were made to determine the effect of the character and quantity of inoculum used. One-year-old apple seedlings were sorted into uniform lots of 10 trees each, 4 incisions were made in each tree, and each wound was inoculated with 1 of 3 types of inoculum. The inoculum was (1) a mass of mycelium and agar from an agar culture, (2) a small chip from an

inoculated heat-sterilized apple twig on which the fungus had been allowed to grow for 2 months, or (3) a piece of twig 2 inches long prepared as in (2). After inoculation, the seedlings were packed in moist peat and held in a cool room (15° to 20° C.). The results of this experiment are given in table 1.

TABLE 1.—*Influence of type of inoculum on infection of apple seedlings inoculated with Xylaria mali, Feb. 2, 1934*

[10 trees inoculated at 4 incisions each]

Type of inoculum	Results on Apr. 27, 1934	
	Incisions infected	Average length of lesions
	Percent	*Mm.*
Mycelium from an agar culture	0	
Small chip of inoculated wood	0	
Small inoculated twig	60	15.6

Under the conditions of this experiment, inoculations with agar-culture inoculum and with a small chip of inoculated wood were not successful; apparently the fungus died before infection took place. A fair percentage of infection resulted when the inoculum was a fairly large piece of infected twig.

EFFECT OF WOUNDING

Field observations indicate that *Xylaria mali* readily attacks apparently uninjured roots, and therefore wounding seems to be unnecessary for natural infection. To determine the influence of wounding on dug trees, inoculations were made on February 2, 1934 on 1-year-old apple seedlings stored in moist peat in a cool room (temperature 15° to 20° C.). The seedlings were divided into 2 comparable lots of 20 trees each. An incision (flap cut) was made in each seedling of 1 lot and a twig culture of the fungus was fastened to it by a rubber band. The other lot was inoculated in the same way but without wounding. The results of the experiment appear in table 2.

This experiment indicates that wounding is not necessary for infection of stored trees by *Xylaria mali*. The fact that fewer infections and smaller lesions occurred on the wounded trees may have been due to the wound callus, which may be less susceptible to attack than normal root tissue.

TABLE 2.—*Effect of wounding upon infection of apple seedlings inoculated with Xylaria mali, Feb. 21, 1934*

[20 trees in each lot]

Host treatment	Results on Apr. 27, 1934	
	Trees infected	Average length of lesion
	Percent	*Mm.*
Inoculum inserted in a flap-cut wound	50	16
Inoculum applied without wounding	80	20

EFFECT OF TEMPERATURE

Two Petri plates of string-bean agar inoculated with *Xylaria mali* (isolate 57) on November 23, 1937, and held at each of the indicated temperatures for 14 days contained mats of the average sizes shown in the following tabulation:

Temperature (° C.)	*Diameter of mat after 14 days*
	Mm.
40	0
35	0
30	65
25	75
20	55
15	17.6
10	9.3
5	0
0	0

The results indicate that, although this isolate will grow in culture at a temperature as low as 10° C., its optimum is near 25°.

In order to learn the effect of temperature on root infection, the roots of yearling apple seedlings were inoculated at two places each with isolate 57 by attaching pieces of twig inoculum without wounding. The seedlings were then wrapped in moist paper, and 12 were put in each of two 8-liter jars. One jar was placed in a controlled-temperature room held at 15.5° C., and the other was held in the laboratory at about 21°. This experiment, run in 1934, was repeated in 1935, and a third lot of seedlings was held at outside temperatures (−3° to 18° C.). The results of these experiments are reported in table 3.

TABLE 3.—*Effect of temperature on infection of yearling apple seedlings by Xylaria mali*

[12 seedlings in each lot]

Temperature (° C.)	Results of Mar. 17, 1934, inoculations (after 2 months)		Results of Mar. 16, 1935, inoculations (after 1½ months)	
	Trees infected	Average length of lesions	Trees infected	Average length of lesions
	Percent	*Mm.*	*Percent*	*Mm.*
−3 to 18 (outside)			0	
15.5 (controlled)	31	16	83	11
21 (room)	84	22	96	21

The data show that *Xylaria mali* will grow on culture media at a temperature as low as 10° C. and that it will infect stored apple seedlings at a temperature as low as 15.5°, which is much lower than that of the top layers of soil during much of the summer where this disease is prevalent. In 1935 the seedlings were in poor condition at the conclusion of the experiment, but they were still alive. Attention should be called to the fact, however, that conditions affecting resistance in trees that have been dug and stored may be different from those in undisturbed trees.

RELATIVE PATHOGENICITY OF DIFFERENT ISOLATES

The relative pathogenicity of different isolates from naturally diseased apple roots was determined by growing them on sterilized apple twigs, which in turn were used to inoculate the roots of stored yearling apple seedlings. In 1933 the seedlings were divided into uniform lots of 10, and in 1934 into lots of 8. Each lot was wrapped in moist paper, packed in moist peat, and placed in a cool room with a temperature range of 15° to 20° C. until the final record, as shown in table 4, was made.

TABLE 4.—*Relative pathogenicity of different isolates of Xylaria mali on yearling apple seedlings*

[10 seedlings inoculated with each isolate on Nov. 30, 1933, and 8 with each on Apr. 6, 1934. Final record made on Jan. 10 and May 18, 1934, respectively]

Year of inoculation and isolate No.	Source of inoculum	Trees infected	Average length of lesion	Year of inoculation and isolate No.	Source of inoculum	Trees infected	Average length of lesion
1933		*Percent*	*Mm.*			*Percent*	*Mm.*
3	Markham, Va	60	22.1	127	Front Royal, Va	100	14
28	Hillsboro, Va	30	19.7	142	Leesburg, Va	100	14
30	Winchester, Va	0		149	do	87.5	18
56	Linden, Va	0		152	do	87.5	14.7
57	Bluemont, Va	100	42.5	158	do	75	11.7
58	do	50	26.4	161	do	87.5	9.7
59	do	70	39.1	164	do	100	14.2
61	Purcellville, Va	30	19.3	168	do	87.5	13.3
63	Leesburg, Va	30	27.3	172	do	100	13.9
				182	do	50	7.7
1934				197	do	0	
29	Charles Town, W. Va	0		198	do	100	20.2
103	Bluemont, Va	0		199	do	75	17
117	Winchester, Va	50	8.5	200	do	100	18.5
126	Martinsburg, W. Va	37.5	6.6				

Table 4 shows great variation in the pathogenicity of 27 isolates from 10 different localities in Virginia and West Virginia. Infection ranged from 0 to 100 percent, and average length of lesion from 6.6 to 42.5 mm. The pathogenicity of the fungus on stored trees might be different from that on trees growing in the field. This experiment, however, suggests that some of the irregular distribution and severity of the disease may be associated with variation in pathogenicity of strains of the organism as well as with edaphic conditions. Fromme (*2*)[2] also found differences in the pathogenicity of isolates.

COMPARATIVE SUSCEPTIBILITY OF APPLE, PEAR, PLUM, CHERRY, AND PEACH TREES

During the greater part of 1933 and 1934 monthly inoculations were made on 3- to 5-year-old seedling trees of apple, pear, plum, cherry, and peach. In the tests made in June and July, the period of greatest susceptibility, at least 20 trees of each species were used at each inoculation period, but at some of the other periods only 5 to 10 trees were inoculated. During a period of high susceptibility 40 to 80 percent of the apple trees and 5 to 10 percent of the pear trees became infected. Many of the lesions on the apple trees were typical deep lesions, but on the pear trees they were shallow and soon healed over.

[2] Italic numbers in parentheses refer to Literature Cited, p. 311.

On young mazzard and mahaleb cherry seedling trees infection would sometimes advance as much as 10 to 20 mm., and by the next year the lesions would have healed over. Fromme (*2*) reported infection from inoculation on apple, pear, cherry, elm (*Ulmus americana*), honeylocust (*Gleditsia triancanthos*), and Norway maple (*Acer platanoides*). Schneiderhan (*5*), in a popular report, stated that oak, maple, hackberry, grape, sassafras, and ash were infected by inoculation. Neither of these workers, however, stated whether the lesions continued to enlarge or whether they soon healed over. However, Schneiderhan did state in recent correspondence:

* * * On the Dutrow orchard near Charles Town, W. Va., Fromme and I found several cherry trees that were dead from *Xylaria mali* after having been planted where an apple tree had been previously killed by the fungus. I strongly suspect that pear trees are also susceptible.

Several hundred inoculations on peach and myrobalan plum seedling trees all gave negative results. In many field examinations the writer has never found *Xylaria* attacking the roots of cherry, peach, or plum trees growing near or interplanted with diseased apple trees. In one instance in the Shenandoah Valley of Virginia, peach trees were planted where apple trees known to be infected with *Xylaria* had been removed, and after 4 years no evidence of black root rot was found on them.

On the other hand, J. O. Andes, of the Tennessee Agricultural Experiment Station, mentioned, in conversation with the writer, that *Xylaria* had effectively attacked a peach tree growing where an apple tree infected with *Xylaria* had been removed. The experiments herein reported and the field observations of the writer seem to bear out the belief that peach, plum, cherry, and possibly pear trees are sufficiently resistant to be grown successfully on land from which a diseased apple orchard has been removed.

SUSCEPTIBILITY OF SEEDLING CLONES AND OF SEEDLING AND OWN-ROOTED APPLE VARIETIES

Experimental plots of trees growing at the United States Horticultural Station, Beltsville, Md., used for testing possible differences in root susceptibility to infection with *Xylaria* were of three types. Part were own-rooted apple varieties, part were clonal lines of seedlings that had shown merit for understock use, and part were seedlings of standard varieties. The own-rooted varieties had been started with nurse roots and had grown for two seasons; the clones of seedling origin had grown for two seasons from root cuttings; and the variety seedlings were 1 year old when obtained for this experiment. The trees were set 2 feet apart in nursery rows 5 feet apart. The plots of own-rooted varieties contained from 9 to 20 trees each. The variety seedling and clone plots contained from 10 to 20 trees, usually 20.

The trees were allowed to grow undisturbed till midsummer of the second year, at which time they were inoculated with twig cultures of *Xylaria* isolate 57 applied to the main root without deep wounding. Only one inoculation was made on each tree in a single year. The results of inoculation were recorded at the end of the growing season, or after October 15. The lesions that developed usually healed over during the following season. By inoculating opposite sides of the roots in successive years, repeated inoculations have been

made. The own-rooted seedling varieties were inoculated for 4 different years and the others for 3 years.

The results of this work are reported in tables 5 to 7, wherein lesions are divided into two main groups—shallow infections of the cortex only and deep infections, which penetrate into the cambium. Cortical infections are the result of host-parasite reactions of such a nature that the fungus attack is checked before the cambium is killed, and these shallow lesions heal much more rapidly than deeper lesions. A high ratio of cortical to deep infections may be an important indication of host resistance.

The sizes of the deep lesions, as given in the last column of tables 5 to 7, were obtained in the following manner: For each lesion, the length was multiplied by the breadth to determine the approximate area. The square root of the resultant area was then derived, giving

TABLE 5.—*Infection and size of deep lesions on young own-rooted apple trees inoculated with Xylaria mali*

[Varietal means from approximately 36 to 80 readings on 9 to 20 trees of each variety; each tree was inoculated in 1936, 1937, 1938, and 1939]

EXPERIMENTAL DATA

Variety	Mean of varieties			
	Total infection	Cortical infection only	Deep infection [1]	Size of deep lesions
	Percent	*Percent*	*Percent*	*Mm.*
Arkansas (Black Twig)	90.0	50.0	40.0	26.2
Ben Davis	75.0	25.0	50.0	21.9
Delicious	91.3	32.4	58.9	32.7
Fallawater	88.9	36.1	52.8	21.0
Golden Delicious	64.3	42.8	21.5	15.6
King David	72.4	43.3	39.1	23.1
McIntosh	78.2	35.2	43.0	20.2
Northern Spy	65.2	23.0	42.2	19.2
Opalescent	60.8	29.6	31.2	28.7
Perkins	75.0	41.1	33.9	18.9
Red Astrachan	70.8	43.5	27.3	14.6
Rome Beauty	50.0	20.8	29.2	13.3
Smith Cider	63.5	28.2	35.3	22.7
Stayman Winesap	91.0	17.5	72.5	34.8
Summer Rambo	89.6	22.9	66.7	27.8
Tolman Sweet	76.1	21.7	54.4	27.9
Wealthy	86.7	23.4	63.3	24.4
Yellow Transparent	68.0	31.3	36.7	20.9
York Imperial	78.6	54.3	24.3	16.1
All varieties: [2]				
1936	47.7	----	22.9	11.1
1937	76.1	----	25.7	16.8
1938	82.3	----	70.0	27.0
1939	95.7	----	54.5	24.0

ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Mean square [3]		
		Total infection	Deep infection	Size of deep lesion
Variety	18	560.53	883.15*	197.04
Years	3	7,735.23**	9,871.94**	1,082.01
Variety × years	54	401.24	430.84	510.15

[1] Twice the standard error of the difference for deep infection is 29.4. A difference between any 2 values, therefore, that amounts to as much as 29.4 is considered statistically significant (19:1).

[2] In yearly means twice the standard error of the difference for percent total infection is 13.0, for percent deep infection it is 13.5, and for size of deep lesion it is 14.8. Differences greater than these values, therefore, are considered statistically significant (19:1).

[3] *=Significant (19:1); **=highly significant (99.1).

a linear value equal to one side of a square having an area proportionate to that of the lesion. The values recorded in the table are averages of such linear functions for all lesions in each designated plot. Since the lesions were irregular in outline and the ratio of surface killing to cambium killing might not be the same, it was difficult to obtain a high degree of accuracy in such measurements. The sizes of deep lesions, therefore, as given in the tables, represent approximate rather than absolute values.

TABLE 6.—*Infection and size of deep lesions on young apple seedling clones inoculated with Xylaria mali*

[Clone means from approximately 30 to 60 readings on 10 to 20 trees of each variety; each tree was inoculated in 1936, 1937, and 1938]

EXPERIMENTAL DATA

Seedling clone No.	Mean of clones			
	Total infection	Cortical infection only	Deep infection [1]	Size of deep lesions
	Percent	*Percent*	*Percent*	*Mm.*
227 [2]	43.5	4.2	39.3	28.1
309	76.9	7.7	69.2	29.3
316	59.4	29.7	29.7	20.1
317	50.8	36.5	14.3	37.4
323 [2]	87.5	19.1	68.5	50.8
329	61.1	36.1	25.0	28.8
1223	48.7	20.5	28.2	17.4
1224	77.7	38.8	38.9	24.2
1225 [2]	78.4	24.8	53.6	31.1
1226	29.2	16.3	12.9	15.5
1227	54.5	40.6	13.9	15.2
1232	50.9	28.7	22.2	23.8
1241	25.0	12.5	12.5	27.2
1249	37.8	17.8	20.0	30.3
1251	48.9	35.6	13.3	23.7
1256	36.4	18.2	18.2	19.3
1258 [2]	30.0	20.0	10.0	12.8
1263	28.2	12.5	15.7	25.7
1267	47.6	26.8	20.8	31.1
1269 [2]	40.9	20.7	18.2	33.9
1271	40.7	22.2	18.5	20.8
1272	26.6	16.6	10.0	28.3
1273	45.7	22.4	23.3	21.6
1283	72.9	36.3	36.6	27.4
1291	58.1	29.3	20.8	12.3
1297	62.4	26.1	36.3	19.2
1299	51.0	16.5	34.5	24.4
1300	52.7	34.9	17.8	23.9
1302	65.9	20.9	45.0	38.1
1303	25.9	18.5	7.4	21.2
All clones: [3]				
1936	26.90		16.67	9.46
1937	47.58		1.25	2.09
1938	69.32		51.19	23.46

ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Mean square [4]		
		Total infection	Deep infection	Size of lesion
Variety	23	643.73	301.96	79.26
Years	2	10,795.18**	12,290.12**	2,828.16**
Variety × years	46	668.57	454.55	102.45

[1] Twice the standard error of the difference for deep infection is 35.0. A difference between any 2 values, therefore, that amounts to as much as 35.0 is considered statistically significant (19:1).

[2] Data lacking for 1 year; not included in the statistical summary.

[3] In yearly means twice the standard error of the difference for percent total infection is 14.9, for percent deep infection it is 12.3, and for size of lesion it is 5.8. Differences greater than these values, therefore, are considered statistically significant (19:1).

[4] **=Highly significant (99:1).

TABLE 7.—*Infection and size of deep lesions on young apple seedlings inoculated with Xylaria mali*

[Varietal means from approximately 30 to 60 readings on 10 to 20 seedlings of each variety; each seedling was inoculated in 1936, 1937, and 1938]

EXPERIMENTAL DATA

Variety	Mean of varieties			
	Total infection	Cortical infection only	Deep infection [1]	Size of deep lesions
	Percent	*Percent*	*Percent*	*Mm.*
Ben Davis	56.4	8.1	48.3	26.8
Delicious	48.1	23.7	24.4	21.8
Fameuse	53.1	14.4	38.7	21.4
Jonathan	58.7	20.5	38.2	19.6
McIntosh	60.3	21.2	39.1	29.6
Northern Spy	47.0	20.1	26.9	21.5
Rome Beauty	44.6	14.4	30.2	20.6
Red Rome Beauty	59.2	11.4	47.8	30.9
Wealthy	44.7	20.8	23.9	34.2
Commercial (mixed)	43.7	6.0	37.7	32.7
All varieties: [2]				
1936	45.63		31.52	26.67
1937	31.95		3.73	6.99
1938	77.27		71.36	27.20

ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Mean square [3]		
		Total infection	Deep infection	Size of deep lesion
Variety	9	133.68	236.57	57.01
Years	2	5,403.55**	11,555.54**	1,326.71**
Variety × years	18	440.76	507.01	124.97

[1] Twice the standard error of the differences for deep infection is 36.8. A difference between any 2 values, therefore, that amounts to as much as 36.8 is considered statistically significant (19:1).

[2] In yearly means twice the standard error of the difference for percent total infection is 18.8, for percent deep infection, it is 20.1, and for size of lesion it is 10.0. Differences greater than these values, therefore, are considered statistically significant (19:1).

[3] ** = Highly significant odds (99:1).

In general, resistance was greater at the first inoculation, and in some cases at the second, than at later ones. Many of the plots showed no deep infections at all from the first inoculation. An entirely adequate explanation cannot now be given for this fact. Evidence points to the conclusion, however, that resistance to infection is more probably associated with host conditions favorable for infection than with environmental conditions unfavorable for the growth of the pathogen. The work in general indicates that young trees are more resistant to infection than older ones. The crowding that obtains in nursery plantings as they grow older probably also tends to make the host less resistant. Resistance has appeared to be associated with vigor. However, Stayman Winesap, which showed outstanding vigor on its own roots, was also outstandingly susceptible, showing a high percentage of infections as well as large lesions. This was true even during the first year of inoculations when the suppressive effect of crowding was less important than it later became.

These inoculations gave wide variation in percentage of infection and also in the average size of the lesions on the different clones. Some clones were more susceptible than others, but none was consistently highly resistant. This record points to the need for con-

tinued intensive testing of possible root stocks for use in areas where *Xylaria* abounds.

The yearly means (tables 5–7) show that the percentage of deep infection for all plots was comparatively low in 1936 and 1937, but much higher in 1938. The one inoculation experiment in 1939 also showed a high percentage of deep infection. The differences in the amount of infection in the different years are probably due to more than one concomitant factor. Earlier experiments have indicated that while the trees in a planting are still young and before competition and crowding are appreciable, a low percentage of infection often results from inoculation. Other contributing factors may have been temperature and moisture. Thermograph records in the field near the experimental plot showed that in 1936 there were only 15 days and in 1937 there were only 12 days from July 15 to September 1, the period after inoculation, that had a temperature as high as 80° F. (26.7° C.), in contrast to 25 days in 1938. Also the mean temperature for this period was only 76.8° F. (24.9° C.) in 1936 and 75.4° F. (24.1° C.) in 1937, while in 1938 it was 79.3° F. (26.3° C.). During the same period there were twice as many days having a daily mean temperature of 80° F. in 1938, the year of high infection, as in 1937, a year of low infection. The temperature studies reported on page 302 indicate that isolate 57, the strain of the fungus studied, is a high-temperature soil organism, the optimum in culture being about 25° C. An examination of the rainfall data for Beltsville, Md., for July and August, 1936, 1937, and 1938 gave no information that would explain the differences in infection in the different years.

These inoculation experiments agree in the main with the West Virginia experiments of Fromme and Schneiderhan (*3*), who reported that—

> No evidence of any promising measure of resistance was exhibited by any one of 45 clons of *Malus* spp. exposed to natural infection, or by any one of 12 clonal stocks and 11 seedling stocks inoculated with *Xylaria mali* in pure culture.

GROWTH AND LONGEVITY OF XYLARIA MALI IN DEAD ROOTS

The question is often asked how long the black root rot fungus can remain alive in the soil and in the roots affected. Several different approaches to a study of the problem of longevity in *Xylaria mali* have been made.

In connection with other studies, at several times early in the summer, twenty 5-year-old apple trees were girdled just above the soil line by removing a zone of bark one-fourth inch wide and in midsummer the roots were inoculated with *Xylaria mali*. Where the roots died as a result of the girdling the lesions were smaller than where the girdled zone was partly closed over and the roots remained alive. Usually there was little enlargement of the *Xylaria* lesions after the death of the infected parts. Possibly harmful products from reactions in the killed host plant make conditions unfavorable for the growth of the fungus.

Other experiments to determine the longevity of *Xylaria* were made by cutting roots, known to contain the viable fungus, into 3-inch lengths. On November 17, 1933, over 100 sections from 38 roots from different infected trees were buried at depths of 3, 6, and 9 inches. After 4 months the viability of the fungus was determined

by placing the roots in moist chambers under conditions favorable for growth of the fungus and attempting to recover it by the usual isolation methods. Very few roots yielded cultures after 4 months, and after a year no viable mycelium was found. Undisturbed roots left in the soil for a year or more after the death of the host often gave negative results when attempts were made to isolate the pathogen. On the other hand, isolation of the pathogen from diseased roots was successful many times; in some cases the fungus was isolated from roots that had remained undisturbed in the soil for at least 4 years after the death of the host. Schneiderhan (*5*) reported a case in West Virginia where *Xylaria mali* remained alive in a root in the soil for 16 years.

These observations and experiments indicate that *Xylaria* often dies soon after the infected root dies. On the other hand, the pathogen may sometimes remain alive in some of the infected roots for a number of years after the death of the host.

A large number of isolation experiments as well as a study of infected roots in the soil and in moist chambers indicate that competing soil organisms may be important in killing *Xylaria mali* in apple roots. A species of *Trichoderma* was very frequently found growing on roots that had been killed by *Xylaria*, as evidenced by the characteristic stroma of *Xylaria*. Attempts to isolate the pathogen from the margins of the diseased areas of such roots often resulted in isolating *Trichoderma* but not *Xylaria*. Microscopic examination of the mycelium of *X. mali* in contact with the mycelium of a species of *Trichoderma* from apple roots in a mixed culture showed a collapse of the mycelium of *Xylaria*. The deleterious action of other soil organisms besides *Trichoderma* may be important in the killing of *X. mali*. Weindling (*7*) reported a lethal effect of *T. lignorum* on *Rhizoctonia solani*.

The origin of *Xylaria mali* is still obscure as is also its relation to other forms of the genus *Xylaria*. A number of different species of *Xylaria* occur throughout the world, but most of them are saprophytic. Lyon (*4*) reported an undetermined species of *Xylaria* as causing a root rot of hibiscus in Hawaii. *X. mali* is not known to occur on either wild or cultivated plants anywhere outside of the eastern and central part of the United States. This suggests that it is indigenous in this region, but a wild host has not been discovered. The wide variation in the pathogenicity of different isolates affords some evidence of transition stages from the saprophytic to the parasitic habit. These considerations suggest the hypothesis that this parasitic species developed from some of the related saprophytic forms present in the region where the disease occurs.

DISCUSSION

Black root rot is serious only in the southeastern and south-central parts of the United States. The regional distribution of the disease may be associated with soil temperature high enough to favor the growth of the pathogen, as indicated by temperature studies on one strain of the fungus.

Local distribution, on the other hand, appears to be at least partly dependent on host conditions. Orchard observations have indicated that the condition of the tree is important. Maturity of the tree and

also an unthrifty condition due to such conditions as overbearing, starvation, or cold injury appear to predispose to infection. Black root rot is essentially a disease of the bearing orchard. Young orchards are seldom affected, although young trees set where diseased ones have been removed usually become diseased. Young replants are subjected to two conditions that may explain their susceptibility: (1) There is an abundance of diseased roots from the removed tree to serve as inoculum; and (2) growing conditions for replants are not good because of competition with established trees and possibly also because of deficiencies of certain salts and an accumulation of toxic substances. Aside from the influence of the factors just mentioned, there are probably physiological changes that make the tree more susceptible after it reaches fruiting age. Overloading with fruit, such as often occurs when bearing is biennial, may result in a weakened tree. The physiological effect of overbearing has been observed by the writer on trees growing in the Pacific Northwest where winter injury of the sunscald type was much more severe on trees bearing an abnormally heavy load of fruit than on those that had been well thinned or that did not bear a crop that year. Similarly, a general weakened condition from overbearing might result in increased susceptibility to black root rot in sections where the disease prevails.

Although the inoculation experiments reported in this paper were carried out on trees of prebearing ages with no anticipation of the importance of age of the host, a review of the experiments shows that infection was more readily accomplished as the trees became older. On 4- to 6-year-old trees, inoculations usually resulted in a fair percentage of cases that made measurable lesions, but these lesions usually healed during the subsequent season. On younger trees, infection was more difficult to accomplish. However, in the region where the disease prevails, when once established on bearing trees, it continues to advance until the tree dies. Change in susceptibility to disease as the host becomes more mature has been shown in phytophthora trunk canker (*1*) and northwestern anthracnose (*6*) of apple.

Inoculation studies on young cherry, peach, plum, pear, and apple trees indicate that the apple is by far the most susceptible host. Small lesions have resulted from inoculation on cherry and pear trees, but they soon healed over. The results of inoculation experiments and of field observations indicate that the disease will probably not become serious on cherry, peach, plum, or pear trees growing in the vicinity of diseased apple trees.

Inoculation of a large number of scion and understock combinations with a virulent strain of the pathogen in pure culture indicates that there is sufficient variation in host susceptibility to justify the hope that resistance to the disease may be obtained by further search for resistant stocks.

SUMMARY

Black root rot of apple has a restricted distribution. It is not known to occur in any country except the United States. Here it is distributed from Pennsylvania to Georgia and westward to Arkansas. Distribution may be partly dependent on the soil temperature's being warm enough for the pathogen to thrive. Local distribution is apparently affected by certain conditions adverse to the host.

In inoculation experiments infection was not successful when the inoculum used was a mass of mycelium from an agar culture; it was successful when the inoculum was infected apple twigs. Field observations and inoculations indicate that wounding is not necessary for infection.

In agar cultures one isolate of *Xylaria mali* made fair growth at 15° C., but its optimum was about 25°. Roots of stored apple seedlings were infected at a temperature as low as 15.5°.

Inoculations with 27 different isolates of *Xylaria mali* indicate that there is wide variation in pathogenicity, as shown by the percentage of infection and the size of lesions produced on roots of yearling apple seedlings.

The relative susceptibility of the apple, pear, plum, cherry, and peach seedlings was determined by inoculation; only the apple showed undoubted susceptibility. Small lesions were produced on the pear and cherry, but these had healed over by the next year.

Tests were made for resistance to *Xylaria mali* in 3 or 4 successive years on 19 own-rooted standard apple varieties, on 30 seedling clones, and on seedlings of 9 named varieties of apples. Analysis of variance showed only slight significance for variety in own-rooted varieties; in the own-rooted seedling clones and variety seedlings there was no significance for variety. The year 1938 had higher temperatures than 1936 or 1937 for the period of 49 days subsequent to inoculations. Statistical analysis of the infection data showed a significant correlation between infection and season with high temperature.

Longevity of the fungus in infected apple roots was variable. In several experiments, the living fungus could not be found a few months after the death of the host. However, in some natural infections it survived the host by several years.

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